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HABITAT AND INTERSPECIFIC INTERACTIONS AFFECT MESOCARNIVORE OCCUPANCY IN THE EASTERN U.S.

by

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THE PURDUE UNIVERSITY GRADUATE SCHOOL
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ABSTRACT

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Interspecific competition is important to carnivore communities because of the propensity of carnivores toward aggressive interactions. Interactions among members of the eastern U.S.A. mesocarnivore community have been impacted by the loss of top predators and urbanization. Changes to interspecific interactions and habitat result in changes in many populations of mesocarnivores. Interactions between these two factors further explain contrasting patterns among the members of the mesocarnivore community. These patterns have been studied at scales from the effects of microhabitat to landscape scale factors on mesocarnivore occupancy, however they have not been studied throughout multiple independent landscapes in the eastern U.S.A. Here, we used presence absence data from camera traps across the eastern U.S.A. to test the effects of habitat and interspecific interactions on members of the mesocarnivore community. We used single- and two-species occupancy models to estimate the contribution of urbanization and competition with coyotes to declines in gray fox populations. We found that increasing coyote abundance was negatively related to gray fox occupancy, but gray foxes did not respond to urban features. Additionally, we used multi-species occupancy models to investigate the effect of habitat on interspecific interactions among five mesocarnivores. We found that increased urbanization reduced the strength of potential intraguild predation on some mesocarnivores. Collectively, our results suggest that neither interspecific interactions nor habitat alone are capable of explaining patterns in the mesocarnivore guild. However, the inability of mesocarnivores to avoid competition with intraguild predators may contribute to declines in some species. While urbanization may have direct negative impacts, urban areas may be important because of reduced competition in more urbanized landscapes. Given the continued urbanization of the eastern U.S.A., these data provide valuable insight into how habitat may impact interspecific interactions, and, ultimately, how interspecific interactions may affect mesocarnivore occupancy.

CHAPTER 1. DOMINANT COYOTES IMPACT GRAY FOX OCCUPANCY ACROSS THE EASTERN U.S.

1.1 Abstract

Gray fox populations in the eastern United States have experienced declines that differ from trajectories of other mesocarnivore populations. One hypothesis to explain these population trends is that gray foxes have had a negative response to urbanization relative to other mesocarnivores. Additionally, gray fox declines may be the result of interspecific interactions, particularly competition with abundant coyotes. Evidence for each of these alternatives has been documented at some spatial scales, however studies have not evaluated how these two factors affect gray fox distributions across their geographic range. We evaluate factors affecting the occupancy of coyotes and gray foxes in the eastern U.S.A. to differentiate between these hypotheses. We used occupancy models across multiple landscapes to test the effects of drivers of behavior - habitat covariates and interspecies interactions on coyote and gray fox occupancy. Additionally, we estimate a coyote abundance index and estimate the effects of increased coyote abundance on gray fox occupancy. Model results indicate that both coyote and gray fox occupancy probabilities were positively related to the amount of forest present but these same models provided no evidence that gray foxes were impacted by urban cover. Additionally, model results indicate that coyote abundance – not occupancy – was negatively related to gray fox occupancy. Based on these results, we concluded that intraguild effects from coyotes contributes more to low gray fox occupancy in the eastern U.S.A. than urbanization.

1.2 Introduction

Medium sized carnivores, or mesocarnivores, benefit from the extirpation of top predators and, often, from being able to exploit urbanized landscapes (Prugh et al. 2009, Bateman and Fleming 2012). The response of mesocarnivores to the removal of large predators, has altered interactions among species in a process termed mesopredator release (Ripple et al. 2014). Increases in one species can have a cascading effect on other species across trophic levels and among communities (Ritchie and Johnson 2009, Estes et al. 2011).

Coyote (*Canis latrans*) populations expanded rapidly in the latter half of the 20th century, in part as a result of mesopredator release (Nowak 1978). Coyotes are successful in urbanizing environments because there are fewer large predators (Berger and Gese 2007, Ripple et al. 2014) and, also, because they prefer habitats with moderate fragmentation (Bekoff 1977, Crimmins et al. 2012). Coyotes may further benefit from urbanization by exploiting human food resources (Fedriani et al. 2001, Morey et al. 2007). In the eastern U.S.A., coyotes may be considered the top predator since larger carnivores are not abundant or are absent (Gompper 2002, Pickett et al. 2011).

Not all mesopredators benefit from the removal of top predators. For example, gray fox (*Urocyon cinereoargenteus*) populations have declined in North America. Through the early part of the 20th century the gray fox's range expanded northward into Canada and encompassed the entire eastern U.S.A. (Fritzell and Haroldson 1982). Between 1980 and 2000, fur trappers reported decreases in gray fox captures (Peck and Heidt 1985, Cypher 1993) and lower capture rates than those for other furbearers (Conner et al. 1983). Ultimately, biologists have reported dramatically decreased gray fox abundance in several studies in the Midwest (Bluett 2006, Willingham 2008, Alessi et al. 2012).

One hypothesis for gray fox population declines is that trophic cascades as a consequence of increasing coyote populations might drive gray fox declines (Fedriani et al. 2000, Estes et al. 2011). The spatial distribution and abundance of each species in a carnivore community is dependent on interactions with other species (Rich et al. 2017). As coyote populations have grown, the opportunities for them to interact with gray foxes in the form of intraguild predation (Polis et al. 1989, Palomares and Caro 1999) and interspecific competition (Polis and Holt 1992, Caro and Stoner 2003) have likely also increased. Similar resource use by coyotes and gray foxes results in competition (Wooding 1984, Cypher 1993) and can precipitate changes in gray foxes' diet (Smith and Danner 1990). Furthermore, in some systems, coyotes are the primary predator of gray foxes (Farias et al. 2005). As a result, despite similar habitat needs, interspecific interactions may facilitate spatial avoidance of coyotes by gray foxes (Chamberlain and Leopold 2005).

Hypothetically, gray fox population declines could also be driven by changing landscape patterns. Urban sprawl impacts wildlife along the wildland-urban interface (Radeloff et al. 2005, Bar-Massada et al. 2014). Gray foxes generally prefer forest habitat and select forests for home ranges and core use areas (Temple et al. 2010, Cooper et al. 2012, Deuel et al. 2017). As these environments come into contact with urban features, urbanization may impact the distribution of gray foxes on the landscape, with decreasing probability of gray fox occurrence nearer to urban areas (Ordenna et al. 2010). Ultimately, gray foxes may be the mesocarnivore least likely to be present in urban areas, therefore increases to the wildland-urban interface may drive gray fox declines (Bateman and Fleming 2012, Lesmeister et al. 2017).

Previous studies of gray fox populations have been conducted at small spatial scales. Studies of coyote (Person and Hirth 1991) and gray fox (Haroldson and Fritzell 1984) home range selection and home range and Leopold 2005) have related habitat use and interspecific interactions to local scale selection (sensu Johnson 1980). Landscape scale habitat studies (sensu Johnson 1980) have also been conducted both for coyotes (Atwood et al. 2004) and gray foxes (Ordenna et al. 2010) and, less frequently, to estimate spatial avoidance between coyotes and gray foxes. Within a single Southern Illinois landscape, coyote occupancy had a negative relationship with gray fox occupancy (Lesmeister et al. 2015), suggesting spatial avoidance within the landscape. It is unclear, however, whether coyotes impact the occupancy of gray foxes across multiple independent landscapes across the eastern U.S.A.

Occupancy modelling is a commonly used method to characterize the distribution or habitat associations of species like coyotes and gray foxes when detection is imperfect (Mackenzie et al. 2002). To better understand species interactions, two species occupancy models (Richmond et al. 2010) were developed to simultaneously model the occupancy of two species and relate them with additional parameters for the occupancy and detection of one species contingent on the presence and detection of another. This two-species parameterization assumes an unequal relationship between the species of interest which makes them most applicable to species who interact in a dominant/subordinate relationship. Coyote and gray fox relationships follow such a pattern with coyote dominant over gray fox numerically and behaviorally.

We used single and two species occupancy models to test two hypotheses for gray fox distribution throughout their range: urbanization lowers habitat suitability resulting in gray fox declines and competition with coyotes results in gray fox declines. We predicted that, if urbanizing landscapes are driving gray fox declines, the probability of occupancy for gray fox will be positively related to forest cover and negatively related to urban cover and the proximity to urban features. Additionally, we predicted that habitat associations of gray foxes will differ from coyotes. Regarding competition with coyotes, we predicted that, if competition with coyote is contributing to gray fox declines, gray fox occupancy would be less likely to occupy sites where coyotes were present and there would be negative relationship between gray fox occupancy and increasing coyote abundance.

1.3 Methods

1.3.1 Study Area

We collected photographic data on wildlife species at 132 sites across the Appalachian region in the eastern U.S.A. (Figure 1.1). An additional 49 sites used for validation expanded the range of states to include Arkansas, Florida, Georgia, and Mississippi. All sites were located in the eastern temperate forest ecoregion (Omernik et al. 2017). This region can be divided into smaller ecoregions. To avoid confusion between these sub-regions and our total study area, when referring to the full extent of our study area, we will use the term eastern U.S.A. Land use in this region has changed dramatically in the preceding 50 years, with urban cover doubling and cropland declining by one fifth to one half (Brown et al. 2005).

1.3.2 Data Collection

We collected data on the presence and absence of coyotes and gray foxes across multiple landscapes in our study area. Data in this study came from The Appalachian Eagle project (http://www.appalachianeagles.org). This project's original goal was to use citizen science based camera trapping to photograph and determine the distribution of Golden Eagles throughout the Eastern U.S.A. The project additionally collected data on many other species, including many mesocarnivores. Additionally, the Appalachian Eagle project is designed to meet the challenges of large scale monitoring efforts (Lindenmayer and Likens 2010). The use of volunteer camera trapping allows researchers to remotely collect data in many landscapes across a large spatial extent (Silveira et al. 2003, Silvertown 2009). Data collected by remote camera trapping can be used to estimate both site occupancy and abundance (O'Connell et al. 2011).

Volunteer participants of the Appalachian Eagle project collected all photographic data used in this study. Volunteers placed cameras on a tree or post approximately 3' from the ground to view as large a portion of the surroundings as possible. Volunteers were asked to select sites that improved the chances of photographing Golden Eagles. Thus, they selected sites near wooded edges or in small clearings and generally at locally high elevations such as on top of a hill.

Volunteers instructed to bait sites with deer carcasses collected as roadkill. At least one carcass was placed at each site in the path of the camera. They were also instructed to operate sites for 2 to 4 weeks sometime between December 1st and April 14th. Volunteers sent all images to the project lead where they were imported into a database and each image was labeled for coyote or gray fox presence. Additionally, we estimated the number of coyote visiting the site each day based on the maximum number of coyote seen in a single image during each day.

The sampling protocol presents several constraints that make the data from this study most appropriate to evaluate occupancy at large scales, but not appropriate to assess local or microhabitat features. First, site selection cannot be considered random because the choice of site was meant to attract eagles. Second, site selection was shaped by the availability or discretion of each volunteer, so sites were often at property that could be easily accessed by the volunteer such as open fields or state land in the case of volunteers who worked for state wildlife agencies. Third, baiting the sites with a strong attractant enhances the detection power of cameras for species present near the site. An attractant will draw animals in from a larger area around the site (Burton et al. 2015). These considerations bias each site toward conditions most suitable for detecting Golden Eagles. However, volunteers consistently placed sites in the optimal location within a landscape to detect species. Since the survey protocol does not affect whether species are present within the landscape, occupancy patterns throughout the eastern U.S.A. should be unaffected.

1.3.3 Habitat Covariates

We began modelling by determining the appropriate scale at which to collect land cover data. The critical range at which landscape features will affect coyote and gray fox occupancy was uncertain given that baiting may result in detections over large distances. To account for this uncertainty, we selected multiple spatial scales as buffers for each site based on the reported home range of coyote and gray fox. Buffers were based on the smallest, average, and largest reported home range size for coyote (Person and Hirth 1991, Bekoff 2003, Atwood 2004) and gray fox (Fritzell and Haroldson 1982, Harrison 1997), resulting in five scales (25 km2, 10 km2, 5 km2, 2 km2, and1 km2), because the largest gray fox and smallest coyote home range were the same. Ultimately, we estimated the scale at which each variable performed best in single species occupancy models by testing each scale and selecting the scale that best fit the data based on Akaike Information Criterion (AIC) values (Slover and Katzner 2016).

We chose predictors characterizing the composition of land cover surrounding each site (Table 1.1). We chose as factors impacting coyote and gray fox presence those habitat covariates that had the most empirical support. We assessed the land cover at each site based on data from the national land cover database (NLCD 2011) (Xian et al. 2011). We drew buffers around each site in the study using the buffer tool in ArcMap 10.2 (ESRI 2011). In each of these buffers, we estimated the percentage of each land cover type using tools in geospatial modeling environment (Beyer 2012). At each scale, we estimated the percentage of forest habitat as the proportion of deciduous, evergreen, mixed and total forest cover at each site (Kays et al. 2008, Temple et al. 2010). We also determined the proportion of urban cover (Lesmeister et al. 2016) and agricultural cover at each site (Gehring and Swihart 2003).

We also collected covariates based on the distance from each camera site to the nearest urban area (Kowalski et al. 2015), road (Riley et al. 2006), and water source (Way et al. 2001). Predicting the impacts of urbanization is complicated by two factors: uncertainty in what components of urban landscapes species respond to and determining what level of human development constitutes urbanization. To resolve this uncertainty, we used multiple covariates to classify distance to urbanization. We used map data for the landscape surrounding each site that incorporated urban boundaries defined by the U.S.A. census bureau (U.S. Census Bureau 2015), all urban cover (NLCD), and only high intensity urban cover (NLCD). The distance from each site to the nearest of each urban classifications was estimated as a separate covariate. Finally, we explored potential thresholds for the effect of urban cover and roads similar to those that have been found for other landscape features (Radford and Bennet 2004). We also estimated the distance from each site to the nearest waterbody (Litvaitis and Shaw 1980, Harrison 1987, Way et al. 2001). Data for the distance to nearest waterbody came from the national hydrography dataset (USGS 2014). The distance from every site to the nearest of these features was obtained using the near tool in ArcMap 10.2. We tested for collinearity between all variables and did not include any two variables with a correlation above 0.7 in a single model (Dormann et al. 2013).

We conducted preliminary analysis of the data to test for spatial autocorrelation among sites. We used a partial mantel test to estimate the distance at which spatial autocorrelation might exist between habitat covariates at the 132 sites sampled during the 2012 sampling year using the “ecodist” package in R (Goslee and Urban 2007). We found potential autocorrelation in the habitat for sites closer than 5000 m. For all pairs of sites within 5000 m of each other, we randomly selected one of the sites and removed it. Therefore, we removed 11 sites, leaving 121 for analysis.

1.3.4 Coyote Abundance Index

We estimated the abundance of coyote at each site to further test the impacts of increased competition with coyote on the occupancy of other mesocarnivores. We used an n-mixture model (Royle and Nichols 2003) to estimate site level abundance based on the maximum number of coyote seen at each site during each sample day. The n-mixture model assumes that each site has a latent abundance that is estimated through repeated daily counts of the number of individuals observed at the site to estimate the detection rate at the site. Based on the record of abundances at each site and the estimated detection rate, our models generated an estimated abundance by assuming abundances were distributed according to a Poisson distribution. N-mixture models have received criticism based on the accuracy of their abundance estimates (Barker et al. 2017). However, for the purposes of our models, even a relative measure of abundance provides inference about the effect of increased coyote abundance. All models for this analysis were run in the "unmarked" (Fiske and Chandler 2011) package in R 3.3.2 (R Core Team 2017).

1.3.5 Ecoregions

We classified each site based upon ecoregion to account for unexplained spatial effects that could be attributed to variation throughout our study area. The extent of our study area included areas in which habitat effects and interspecific interactions could potentially differ. This presents a problem because mesocarnivores may respond to these factors differently in different ecoregions. These differences can potentially mask the significance of a covariate or even change the direction of the effect. We collected ecoregion data to check the study sites for stationarity (Wagner and Fortin 2005). We determined which level III Omernik ecoregion (Omernik et al. 2017) in which each site was situated and tested the performance models within each region.

1.3.6 Modelling Overview

We used a multi-stage modelling approach to fit covariates to single- and two-species occupancy models (Gompper et al. 2016). To understand the impact of habitat on the occupancy of coyotes and gray foxes, we tested habitat covariates in single-species coyote and gray fox occupancy models. This process involved three steps. In step 1, we generated the best detection model for coyote and gray fox detection. In step 2, we estimated the scale at which each habitat covariate performed best. In step 3, we tested the effects of those appropriately-scaled habitat covariates on coyote and gray fox single-species occupancy. To understand the effect of competition with coyotes on gray foxes, we compared the performance of gray fox habitat models with models including the covariate coyote abundance index. Finally, we used all covariate sets that appeared in the top single-species models as covariate sets in two-species models (Richmond et al. 2010). At every step, we ranked models with Akaike's Information Criteria (Burnham and Anderson 2002). We standardized beta coefficients from each model based on partial standard deviations (Cade 2015) and averaged coefficients of the effect of each covariate on coyote and gray fox occupancy across all models (Arnold 2010).

1.3.7 Testing the Impacts of Habitat Covariates

To test the effects of habitat on coyote and gray fox occupancy, we fit habitat models in a three step approach. In step 1, we obtained the best estimate of detection from single-species models based upon the habitat at each site. We held occupancy constant and compared all combinations of habitat covariates in coyote and gray fox detection models. The top species-specific detection model was used in each remaining step. In step 2, we evaluated the performance of each proportional land cover covariate at all five scales by testing each proportion land cover covariate at every single scale in single-species models. We selected the most appropriate scale for each covariate based on which model performed best and retained only this scale in the next step. In step 3, we fit models of single-species coyote and gray fox occupancy based upon habitat. We fit models containing all combinations of habitat covariates for each species. We considered all models within 2 ΔAIC as the top performing habitat models. We assessed the significance of each habitat covariate based on the performance of models containing that covariate and whether the 95% confidence interval for the beta coefficient of effect for that covariate overlapped 0.

1.3.8 Testing the Effects of Competition with Coyotes

To understand the impacts of competition with coyote on gray foxes, we tested the impacts of increased coyote abundance on gray fox occupancy and tested the impacts of coyote presence on gray fox occupancy in two-species models. We included the coyote abundance index from n-mixture models as a covariate in all gray fox single-species models. We compared the performance of models including coyote abundance index with those with only habitat. We determined the importance of increased coyote abundance on gray fox occupancy based on whether the 95% confidence interval for the beta coefficient of effect overlapped 0. We used covariates from top coyote and gray fox single-species models as covariates in two-species models. We compared the predicted occupancy of gray foxes conditional on the presence of coyote with the occupancy of gray foxes in the absence of coyote.

1.3.9 Predictive Maps

After generating models with data from 2012, we used significant covariates to predict the occupancy probability of coyotes and gray foxes for areas not part of our original sample. We generated predictive maps of gray fox occupancy using Raster Calculator in ArcMap. We calculated the predicted occupancy throughout the study area as a function of significant predicted covariates. We estimated the proportion of forest cover for the entire study area based on data from NLCD and estimated coyote abundance for the study area by interpolating from the sampled locations. We only attempted to predict the occupancy of gray foxes for areas where predictors were within the range of the original covariates (Figure 1.5).

1.3.10 Validation

We validated models using presence/absence data collected during 2013 to assess the ability of models to predict occupancy based on habitat. Volunteers collected data at 128 sites during this year, of which 80 had not been sampled previously. From this group of 80, 49 were used in the final analysis after removing sites that overlapped previous sites. We generated predicted occupancy probabilities based upon the covariate data collected at each additional site. We compared the predicted occupancy to the true occupancy, which was determined based on whether coyote or gray fox were observed at the site. We produced ROC curves using the r package “MASS” (Venables and Ripley 2002) and calculated AUC values determine the performance of each model. We compared the ability of these models to predict the occupancy of novel sites with the ability of models to predict the occupancy of the original sites. Of the 121 sites used to generate models, 48 were resampled during 2013 for the occupancy of gray foxes and coyotes. We produced ROC curves to compare the predicted occupancy at these sites with true occupancy, and calculated AUC values.

1.4 Results

1.4.1 Coyote Detection

We detected coyote at 111 of 121 sites (91.74%) within the study area. We obtained the best estimate of detection with the model containing the covariates: distance to urban boundary, distance to road, proportion of mixed forest cover, proportion of evergreen forest cover, and proportion of urban cover. The variables proportion of mixed forest cover, evergreen forest cover, and urban cover performed best at scales of 25 km2, 1 km2, and 10 km2 respectively. From this top model, the daily detection probability across all models was 0.3206 (SD = 0.1880).

1.4.2 Coyote Habitat

Our single-species occupancy analysis revealed only a few factors strongly influencing the occupancy of coyotes. Comparison across scale for occupancy covariates revealed that the largest reported home range for coyote, 25 km^2, performed best for all habitat variables. Our results suggested that proportion of total forest cover was a consistent and significant factor impacting coyote occupancy and that distance to water was partially supported as a predictor of coyote occupancy. Four single species coyote occupancy models performed within 2 ΔAIC of the top model with five covariates present in at least one top model (Table 1.2). All top performing single species occupancy models included the variables proportion of total forest cover and distance to water. Model averaging of beta parameters revealed proportion of total forest cover was the only covariate that significantly impacted coyote occupancy (Figure 1.2). Total forest cover was positively correlated with probability of coyote occupancy ($\beta = 1.72$, SE = 0.80). The relationship between habitat covariates and coyote occupancy did not differ significantly between sub-regions (Table 1.6). Additionally, the model-averaged coyote occupancy probability per 25 km^2 block was 0.9372 (SD = 0.1570).

Ten two species occupancy models performed within 2 ΔAIC of the top model (Table 1.4). Total forest cover and distance to water were covariates in all top models and, consistent with single-species models, model-averaging revealed that proportion of total forest cover was the only significant predictor of coyote occupancy ($\beta = 1.77$, SE= 0.87) (Figure 1.3).

1.4.3 Gray Fox Detection

We detected gray fox less frequently than coyote throughout the study area. We detected gray fox at 39 of the 121 sites (32.23 %). Top detection models included the covariates: distance to nearest road, distance to nearest urban boundary, distance to nearest waterbody, proportion of urban cover, and proportion of mixed forest cover. Proportion of mixed forest cover and urban cover performed best at the scale of 2 km^2 and 1km^2 respectively. In our preliminary analysis of gray fox occupancy, we found that proportion of total, mixed, and evergreen forest performed best at the largest possible scale, 25 km^2 around the camera site. Only proportion of urban cover performed best at a smaller scale, 2 km^2. All top performing models contained at least the two variables total forest cover and distance to water. From this top model, the daily detection probability for gray foxes was 0.1799 (SD = 0.1491).

1.4.4 Gray Fox Habitat

Total forest cover and distance to water both had a strong impact on gray fox occupancy, but urbanization had no impact on gray fox occupancy. Six single-species occupancy models performed within 2 ΔAIC of the top model (Table 1.3). Proportion of total forest cover and distance to water were present in all top models. Additionally, total forest cover and distance to water were significant predictors of gray fox occupancy (Figure 1.2). Total forest cover was positively related to gray fox occupancy (β =0.71, SE= 0.29), and distance to water (β = -0.86, SE = 0.30) was negatively related to gray fox occupancy. Proportion of urban cover and distance to urban features each appeared in only one model and neither variable was significant. The relationship between habitat covariates and gray fox occupancy did not differ significantly between sub-regions (Table 1.6). The model-averaged occupancy probability across all models was 0.348 (SD = 0.1935). All top two-species gray fox occupancy models included the habitat covariates total forest cover and distance to water, however only total forest cover was significant (β = 0.71, SE= 0.32) (Figure 1.3).

1.4.5 Effect of Coyotes on Gray Foxes

We found evidence that increased coyote abundance negatively impacted gray foxes. We found that the best single-and two-species gray fox occupancy models all contained the covariate coyote abundance index (Table 1.3 and 1.4). Coyote abundance index was a significant predictor and had a negative effect on gray fox occupancy in single-species models (β = -0.57, SE = 0.28) (Figure 1.3). Two species models did not provide valuable information regarding the interaction between gray fox occupancy and coyote presence. We found that all sites where gray foxes were present were also occupied by coyote. Therefore, the occupancy of gray foxes was always predicted to be higher in the presence of coyote as a result of overlap of the distribution of coyotes and gray foxes at this scale. In two species models, coyote abundance index was negatively related to gray fox occupancy conditional on the presence of coyote, however the magnitude of effect was larger than in single-species models. (β = -1.75, SE= 0.38).

1.4.6 Model Validation

We found that models performed well for predicting coyote and gray fox occupancy at novel sites. Coyote models generally performed better than gray fox models. For coyote models, the top model including total forest cover, and distance to water had an AUC score for novel sites of 0.714. For gray fox models, the top model including total forest cover, distance to water, and coyote abundance had an AUC scores for novel sites of 0.698

Overall, models performed better at trained sites than novel sites in model validation. For coyote models, the best model including total forest and distance to water had an AUC score of 0.911 for trained sites. For gray fox models, the best model including total forest, distance to water, and coyote abundance, had an AUC score of 0.824.

1.5 Discussion

Consistent with our first hypothesis, we observed a negative relationship between increased coyote abundance and gray fox occupancy. These results indicate that the distribution of gray foxes may be limited by coyote because of competition or the threat of predation. There is good evidence of coyote and gray fox interactions including competition and spatial avoidance (Fedriani et al. 2000, Chamberlin and Leopold 2005), however empirical evaluation of these patterns have not been conducted in multiple landscapes across the eastern U.S.A. and results do not always support expectations given competition between these species (Neale and Sacks 2001). Our results are consistent with local and landscape scale studies that indicate gray fox space use was negatively affected by coyotes (Cypher 1993, Chamberlain and Leopold 2005, Lesmeister et al. 2015). These results support our hypothesis that coyotes contribute to gray fox declines, however, at this scale, coyote abundance, not presence, is significant.

Contrary to our second hypothesis, we found that the proportion of urban cover and distance to urban features had no significant effect on either coyotes or gray foxes throughout the eastern U.S.A. Coyotes and gray foxes had similar habitat preferences at this scale, with proportion forest cover being the strongest habitat predictor of occupancy. In part, the limited effect of many landscape covariates on coyote occupancy may be attributed to coyote tolerance of urban environments (Bateman and Fleming 2012) and fragmentation (Crimmins 2012), which contributes to their high occupancy throughout the study area. We predicted gray fox occupancy would be negatively related to urbanization, because gray foxes are known to avoid urban features and are among the North American mesocarnivores least frequently found living in urbanized settings (Ordenna et al. 2010). Our results suggest that, despite this, gray fox occupancy probability was not lower in more heavily urbanized landscapes. This finding may reflect the range of urbanization throughout the extent of our study area. Sites were located within a limited range of urbanization along the wildland-urban interface. This pattern reflects the fact that our sampling design required locating cameras at sites that would attract Golden Eagles, so we did not have sites in predominately urban areas.

Gray fox occupancy was positively related to forest cover, however, our results suggest that the proportion of forest cover in the eastern U.S.A. was high enough to support gray foxes in the absence of coyote. When considering only habitat, we found that the predicted gray fox occupancy probability was generally above 0.5 (Figure 1.5). However, by including the coyote abundance index, we found low predicted gray fox occupancy throughout the eastern U.S.A. Competition with coyote may be contributing to gray foxes declines even in areas of high forest cover. When the coyote abundance index was greater than an estimated five coyotes, gray fox occupancy probability was predicted to be 0 regardless of forest cover (Figure 1.4).

We did not find differences in the effect of covariates between the sub-regions in our study area. Given the extent of our study area, we considered that there may be variability in our data related to spatial effects not explored in our occupancy analysis (Wagner and Fortin 2005). Coyotes and gray foxes have geographic ranges greater than the extent of the eastern U.S.A. Coyotes and gray foxes may exhibit differences between eastern and western U.S.A. populations (Way 2007). While our study area comprised only the eastern U.S.A., habitat potentially may have impacted these two species differently due to heterogeneity in these relationships. However, we found that the relationship between habitat covariates and each species occupancy probability did not differ between these sub-regions. Non-stationarity has been shown to impact model performance for other species or in other systems (Gering et al. 2003, Osborne et al. 2007). In contrast to these studies, our results support the idea that in the eastern U.S.A and at the scale of our study, coyotes and gray foxes responded to habitat consistently.

Our results most strongly differ from smaller scale studies in that we never found gray foxes at sites where coyote were absent. These studies have routinely found that coyote presence impacts gray fox occupancy (Gompper et al. 2015, Lesmeister et al. 2015). Consistent with these studies, we never observed coyotes and gray foxes in the same picture, suggesting possible temporal niche partitioning exists between the two species (Schuette et al. 2013). At the scale of our study, coyote may be present across the entire eastern U.S.A. because of the loss of top predators resulting in the decreased ability of gray foxes to avoid coyotes. Additionally, overlap in the habitat needs of coyotes and gray foxes may result in the inability of gray foxes to avoid landscapes containing coyote by selecting alternative habitat (Gosselink et al. 2003). Presumably, gray foxes attempt to live in landscapes occupied by coyote but are unable to when competition or predation from coyote is most intense in landscapes where coyote are abundant. Novel approaches to modelling occupancy would be useful to examine how the strength of competition may change as a function of habitat (Rota et al. 2016).

Intense competition has not contributed to declines of other mesocarnivores in the same way it has driven declines of gray foxes. Competition between coyote and other mesocarnivores has been noted, including red foxes (Major and Sherburne 1987) and raccoons (Gehrt and Prange 2007). However, these species have not experienced the same declines that gray foxes have. While gray foxes were unaffected by urbanization, other species may use urban areas to avoid competition with coyotes. Abundant human food resources in urban settings may facilitate the coexistence of large numbers of coyotes and other mesocarnivores (Baker and Harrison 2007, Bateman and Fleming 2012). In contrast, gray foxes rely on trees for predator avoidance (Kurta 2004) and may be relatively less likely to use human resources than other mesocarnivores (Fedriani et al. 2001). Body size may also contribute to the strength of interactions between gray fox and coyote (Sepulveda 2013). Mesocarnivores that are more capable of competing with coyote directly or indirectly will not be as strongly affected. However, red foxes have not experienced a decline on par with gray foxes, despite similar body size and predation from coyote (Palomares and Caro 1999). While coyote likely compete with other mesocarnivores, competition has only driven declines of gray foxes.

Ultimately, gray fox populations may be affected by urbanization, however, at the landscape scale, competition between coyote and gray foxes likely drives the spatial structure of gray fox distributions. While we cannot say how urbanization has affected gray foxes, it is likely that loss of forests associated with urbanization has contributed to declines in the presence of gray foxes. Future anthropogenic changes to the landscape will continue to impact gray fox distributions, particularly if they result in the loss of forests or increased coyote abundance.

1.6 References

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Table 1.1 Covariates of the occupancy and detection of coyote and gray fox in the Eastern United States. Habitat covariates include measures of the proportion of the landscape surrounding each site belonging to a particular cover type and the distance from each site to the nearest habitat feature. Proportion landscape variables were all assessed at five scales measuring 1km2, 2km2, 5km2, 10km2, and 25km2, but are reported for the largest range. Distances are in meters.

Covariate	Mean	SD	Max.	Min.	Source
Proportion Total Forest Cover	0.751	0.263	0.996	0.00552	Kays et al. 2008, Temple et al. 2010
Proportion Deciduous Forest Cover	0.657	0.259	0.983	0	Kays et al. 2008, Temple et al. 2010
Proportion Evergreen Forest Cover	0.0467	0.067	0.400	0	Kays et al. 2008, Temple et al. 2010
Proportion Mixed Forest Cover	0.0468	0.0718	0.508	0	Kays et al. 2008, Temple et al. 2010
Proportion Agriculture Cover	0.121	0.171	0.851	0	Gehring and Swihart 2003
Proportion Urban Cover	0.0472	0.0475	0.351	0.000658	Cove et al. 2012, Lesmeister et al. 2016
Distance to nearest water source	1,328	1108	4,628	27	Litvaitis and Shaw 1980, Harrison 1987
Distance to nearest urban boundary	14,037	10,694	46,239	460	Kowalski et al. 2015
Distance to nearest high intensity urban cover	2,447	1,908	11,136	147	Kowalski et al. 2015, Ordenna et al. 2010, Gompper et al. 2016
Distance to nearest of any urban cover	1,176	913	3,994	56	Kowalski et al. 2015, Ordenna et al. 2010, Gompper et al. 2016
Distance to nearest road	3,317	2,483	12,578	56	Riley et al. 2006
Coyote Abundance Index	3.22	2.39	12.80	0.00014	Lesmeister et al. 2016

Table 1.2 Top models for coyote single species occupancy. Models were included here if they performed within 2 ΔAIC of the top model. Included for each model is the name, ΔAIC, the model weight (w), the number of parameters (k), and -2 log-likelihood (-2LL).

Coyote Single Species Occupancy Models	ΔAIC	w	k	-2LL
Total Forest, Mixed, Distance to Water	0	0.2284	13	4388.08
Total Forest, Distance to Water	0.38	0.1889	12	4390.46
Total Forest, Evergreen, Distance to Water	0.44	0.1833	13	4388.52
Total Forest, Distance to Road, Distance to Water	1.65	0.1001	13	4389.73

Table 1.3 Top models for gray fox single species occupancy. Models were included here if they performed within 2 ΔAIC of the top model. Included for each model is the name, ΔAIC, the model weight (w), the number of parameters (k), and -2 log-likelihood (-2LL).

Gray Fox Single Species Occupancy Models	ΔAIC	w	k	-2LL
Total Forest, Distance to Water, Coyote Abundance Index	0	0.1415	13	1479.43
Total Forest, Urban, Distance to Water, Coyote Abundance Index	1.21	0.0773	14	1478.64
Total Forest, Evergreen, Distance to Water, Coyote Abundance Index	1.71	0.0602	14	1479.14
Total Forest, Mixed, Distance to Water, Coyote Abundance Index	1.72	0.0599	14	1479.15
Total Forest, Distance to Water, Distance to Urban, Coyote Abundance Index	1.97	0.0528	14	1479.40
Total Forest, Distance to Water, Distance to Road, Coyote Abundance Index	2	0.0520	14	1479.43

Table 1.4 Top models for gray fox two species occupancy. Models were included here if they performed within 2 ΔAIC of the top model. Covariates listed under coyote occupancy were predictors for only coyote occupancy probability and covariates listed under gray fox occupancy were predictors for only gray fox occupancy probability in the respective model. Included for each model is the name, ΔAIC, the model weight (w), the number of parameters (k), and -2 log-likelihood (-2LL).

Coyote Occupancy	Gray Fox Occupancy	ΔAIC	w	K	-2LL
Total Forest, Mixed, Distance to Water	Total Forest, Distance to Water, Coyote Abundance	0	0.1188	41	5671.94
Total Forest, Distance to Water	Total Forest, Distance to Water, Coyote Abundance	0.69	0.0841	40	5674.63
Total Forest, Mixed, Distance to Water	Total Forest, Distance to Water, Distance to Road, Coyote Abundance	0.95	0.0739	42	5670.89
Total Forest, Mixed, Distance to Water	Total Forest, Urban, Distance to Water, Coyote Abundance	1.2	0.0652	42	5671.14
Total Forest, Distance to Water, Distance to Road	Total Forest, Distance to Water, Coyote Abundance	1.25	0.0636	41	5673.19
Total Forest, Mixed, Distance to Water	Total Forest, Mixed, Distance to Water, Coyote Abundance	1.58	0.0539	42	5671.52
Total Forest, Distance to Water	Total Forest, Distance to Water, Distance to Road, Coyote Abundance	1.65	0.0521	41	5673.59
Total Forest, Distance to Water	Total Forest, Urban, Distance to Water, Coyote Abundance	1.89	0.0462	41	5673.83
Total Forest, Mixed, Distance to Water	Total Forest, Distance to Water, Distance to Urban, Coyote Abundance	1.89	0.0462	42	5671.83
Total Forest, Mixed, Distance to Water	Total Forest, Evergreen, Distance to Water, Coyote Abundance	2	0.0437	42	5671.94

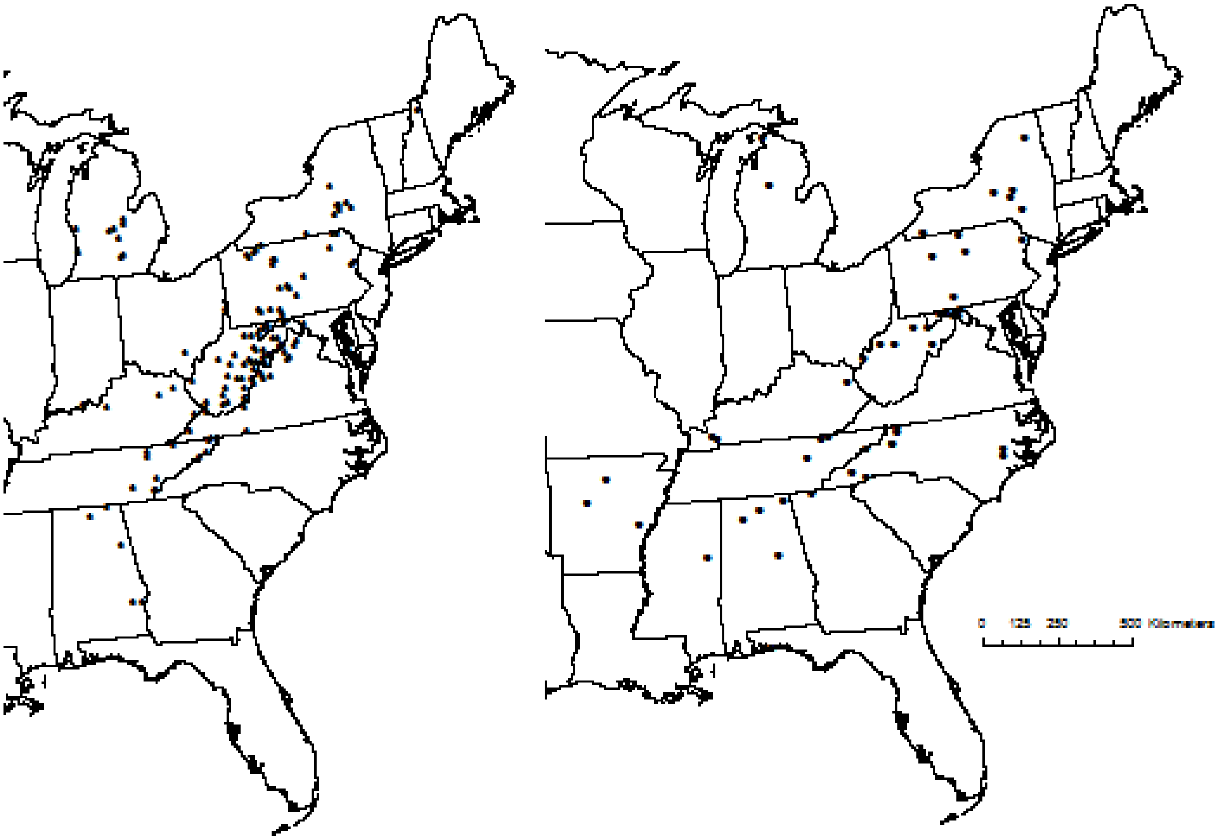

Figure 1.1 Distribution of sites throughout the study area in the Eastern U.S.A. Original sites (left) and validation sites (right).

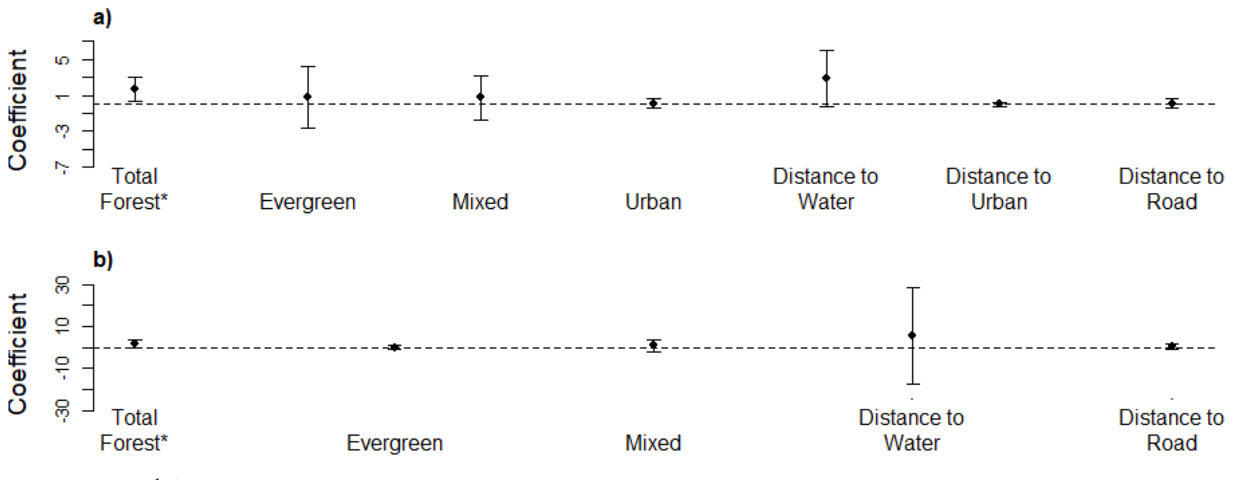

Figure 1.2 Standardized beta coefficients for the occupancy of coyote from single species (a) and two species (b) occupancy models. Points represent the model averaged coefficient of the occupancy probability for each covariate and error bars present the full 95% confidence interval.

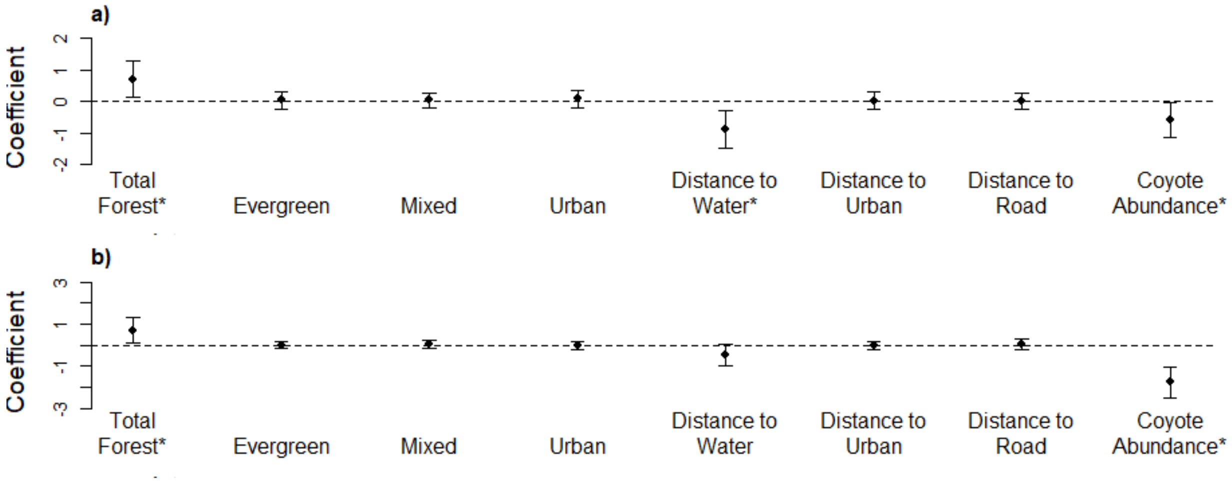

Figure 1.3 Standardized beta coefficients for the occupancy of gray fox from single (a) and two species (b) occupancy models. Points represent the model averaged coefficient of the occupancy probability for each covariate and error bars present the full 95% confidence interval.

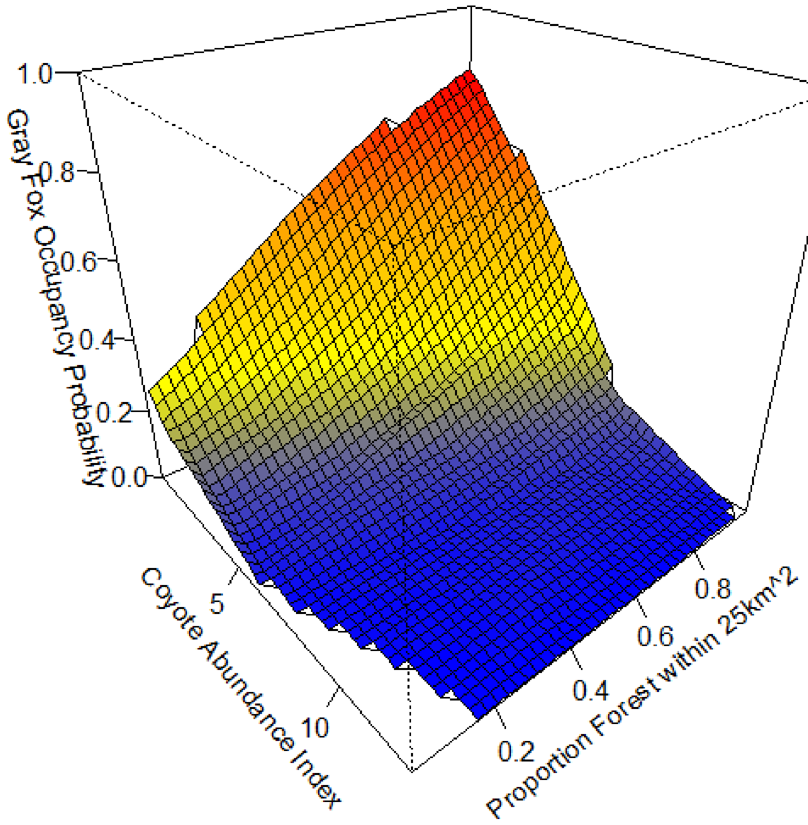

Figure 1.4 The relationship of the proportion of forest cover and the coyote abundance index to the occupancy probability of gray foxes. At low coyote abundance, forest cover impacted gray fox occupancy, but above 5 estimated coyotes gray fox occupancy was always 0.

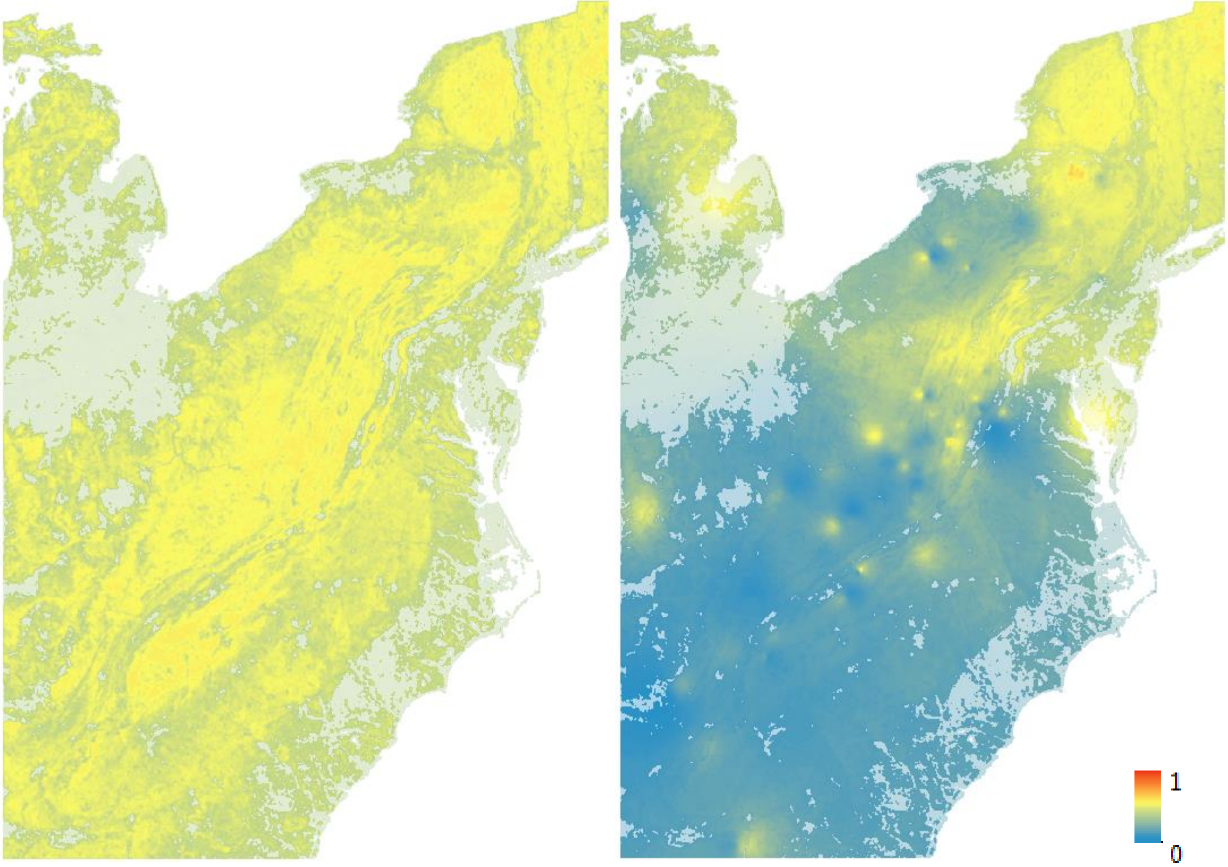

Figure 1.5 Predicted occupancy maps for gray foxes based solely on habitat (left) and habitat plus the coyote abundacne index (right). Predicted occupancy is based on significant predictors from top gray fox models.

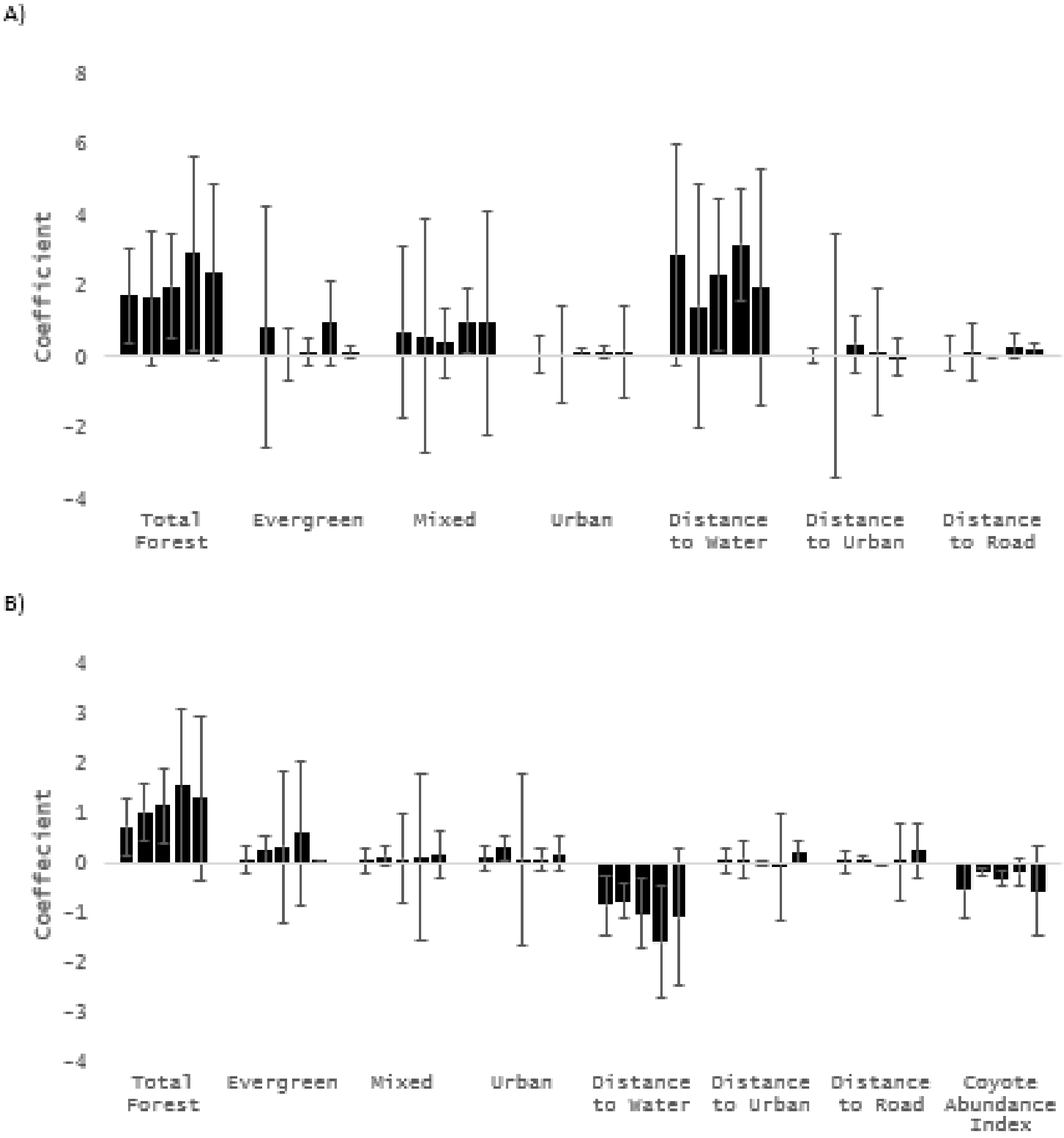

Figure 1.6 Performance of habitat covariates in across sub-regions for coyotes (A) and gray foxes (B) (Omernik et al. 2017). The study area was divided into sub-regions and the performance of models was tested on the subset of sites contained within this sub-region. Coefficients are included for the entire study area and for each sub-region. Models and covariates did not perform significantly different in differing sub-regions implying there was not unaccounted for spatial heterogeneity.

CHAPTER 2. EFFECTS OF HABITAT ON MESOCARNIOVRE INTERACTIONS IN THE EASTERN U.S.A.

2.1 Abstract

The mesocarnivore community in the eastern U.S.A. has experienced changes related to human development including the loss of top predators and urbanization. These changes impact major two factors that contribute to the structure of the mesocarnivore community, habitat and interspecific competition. Many studies examine one or both of these factors, however little is known about how competition and habitat interact. Competition may decrease as habitat quality increases because of greater resources. Competition may additionally decrease in urbanized areas due to human food or habitat fragmentation. We evaluate how interspecific interactions within the mesocarnivore community change as a function of habitat. We used multi species occupancy models across multiple landscapes to test the effects of habitat on interspecific interactions in mesocarnivore occupancy. We estimate the effect that habitat has on five eastern U.S.A. mesocarnivores. We additionally evaluate the strength and nature of interspecific interactions between these species. Finally, we estimate the effect of habitat on interactions between species with strong and weak interactions. Model results indicate that habitat impacted interactions between potential intraguild predators and potential intraguild prey most strongly. In general, competition decreased with increasing habitat quality. Increasing urbanization was positively related to the co-occupancy of only potential intraguild predators and prey. Based on these results, we concluded that mesocarnivores selected habitat that reduced the strength of interspecific competition and intraguild predation. Specifically, potential intraguild prey used urban areas as refuges from competition if they were able to tolerate urbanization.

2.2 Introduction

Interspecific interactions between members the mesocarnivore community impact the spatial distributions of these species. Mesocarnivores interact aggressively through competition (Caro and Stoner 2003) and intraguild predation (Fedriani et al. 2000), both of which reduce the ability of a mesocarnivore population to persist in the presence of larger competitors (Mumma et al. 2017). Particularly, smaller or lower trophic level species respond behaviorally to intraguild predation (Berger and Gese 2008). Top predators may regulate the coexistence of mesocarnivores through top down effects (Sergio et al. 2008). Mesocarnivores may also regulate themselves through resource partitioning (Chesson 2000). Whether due to fear, resource partitioning, or local extirpation, mesocarnivores at lower trophic levels frequently alter their space use in response to interactions with mesocarnivores at higher trophic levels. Therefore, competition and predation impact mesocarnivore communities in a way that is reflected in the space use of all mesocarnivore species.

The mesocarnivore community in the eastern U.S.A. has experienced reduced top down regulation due to the loss of large carnivores resulting in changes to the way species interact. Human persecution and urbanization have caused the extirpation of large carnivores resulting in mesopredator release (Prugh et al. 2009, Ripple et al. 2014). Mesopredator release may result in increased abundance or a larger distribution for species that benefit from reduced direct predation. However, mesopredator release may also result in a trophic cascade in which intraguild predation and competition negatively impacts smaller mesocarnivores (Cove et al. 2012). Ultimately, mesopredator release may increase the strength and importance of these intraguild predator prey relationships between mesocarnivores. Specifically, larger mesocarnivores such as coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) may fill the role of top predator in this system through increased intraguild predation (Gompper 2002). While bobcats may be killed by coyote when resources are low (Wilson et al. 2010), they are most likely to occupy a similar role as a potential intraguild predator of other mesocarnivores (Litvaitis and Harrison 1989, Witczuk et al. 2015). Negative top down effects are most likely to impact smaller potential intraguild prey such as gray foxes (*Urocyon cinereoargenteus*) and red foxes (*Vulpes vulpes*). These species engage in competitive or predatory interactions with coyotes and bobcats (Fedriani et al. 2001, Newsome and Ripple 2014) and may alter their space use in response (Major and Sherburne 1987, Chamberlain and Leopold 2004). Raccoons are often less affected by intraguild predation due to generalist behavior that allows them to coexist with other mesocarnivores (Prange et al. 2003, Beasley 2007, Kowalski et al. 2015). The eastern U.S.A. may contain other carnivores including many avian predators (Terraube and Bretagnolle 2018), striped skunks (*Mephitis mephitis*), and Virginia opossums (*Didelphis virginiana*). These species are not considered because they are not part of the mammalian mesocarnivore guild or occupy a similar role as raccoons.

Human development has additionally resulted in increased urbanization of the landscape, and the status of each member of the mesocarnivore community may also be related to their response to urbanization (Ordenna et al. 2010, Bateman and Fleming 2012). Mesocarnivores may respond positively to urbanization if they are able to make use of anthropogenic resources (Fedriani et al. 2001, Newsome et al. 2012). However, urbanization poses many direct negative effects including habitat loss, habitat fragmentation, and anthropogenic mortality (Bar-Massada et al. 2014). Ultimately, the success of a mesocarnivores in urbanizing landscapes is likely to be the result of their species habitat needs. Coyotes prefer mixed forests with moderate levels of fragmentation (Person and Hirth 1991, Atwood et al. 2004) and therefore may tolerate urbanization (Gehrt et al. 2009). Bobcats generally have much larger home ranges than other mesocarnivores and tolerate urbanization less than coyotes (Riley 2003, 2006). Gray foxes may avoid urban features due to greater need for trees (Bateman and Fleming 2012, Cooper et al. 2012). Compared to gray foxes, red foxes reside in urban and suburban areas more frequently (Lombardi et al. 2017). Raccoons are habitat generalists, capable of using anthropogenic habitat and food sources (Prange et al. 2003).

Increased intraguild predation and urbanization impact the distributions of mesocarnivores, however neither can explain these spatial patterns alone (Rich et al. 2017). Many studies of these two factors compare their relative importance, however the full impact of these factors also depends on how habitat and competition interact (Elmhagen and Rushton 2010, Gompper et al.2016). Interspecific interactions may change as a function of habitat and competition with other species may drive habitat selection (Crete et al. 2001). Urbanized landscapes may reduce the strength of competition an predation even when the direct impacts of human modification are negative. When few top predators persist, human caused mortality decreases the survival of some intraguild predators (Kamler and Gipson 2004, Ordenna et al. 2010). Areas that are in contact with urban or agricultural cover may contain refuse or crops that serve as food resources (Fedriani et al. 2001). With greater influence of urbanization carnivores may compete less for food or maintain smaller home ranges resulting in decreased competition (Salek et al 2014). Differences in habitat suitability may also affect interspecific interactions. In suitable habitat, species may be able to coexist because of plentiful resources, however in resource poor habitats competition may increase. Therefore, interspecific interactions may reinforce habitat suitability patterns, or habitat and interspecific interactions may have opposite effects because of relatively habitat suitability.

To understand how mesopredator release and urbanization impact the mesocarnivore community, there is a need to consider how habitat impacts interactions among all members of the mesocarnivore community and across multiple independent landscapes in the eastern U.S.A. Many studies aim to determine the relative strength of habitat or interactions in structuring the mesocarnivore community. However, previous studies of the interactions between mesocarnivores have been limited in their ability to assess how interactions may change as a function and assess the roles of each member of the community simultaneously (Mackenzie et al. 2014, Gompper et al. 2016). Additionally, studies of mesocarnivore occupancy have evaluated the spatial structure of the mesocarnivore community within a single landscape (Kowalski et al. 2015, Lesmeister et al. 2015). However, mesocarnivores interact across multiple independent landscapes implying the potential for spatial structure across the eastern U.S.A. Here, we used a multi-species occupancy model to investigate how urbanization impacts competition and predation between five mesocarnivores across multiple landscapes in the eastern U.S.A.

We hypothesized that mesocarnivores would select habitat that reduces the strength of competition and that intraguild prey would use urban habitat to reduce the strength of intraguild predation. To test this hypothesis, we assessed the habitat associations of each species, tested the significance of interactions between each species pair, and estimated the effect of changes in habitat on interactions. We expected that, mesocarnivores would vary in their habitat associations due to differences in their responses to urbanization. We predicted that bobcat and gray fox occupancy will be negatively related to urban features while red fox and raccoon occupancy will be positively related to urban features. Based on the nature of interspecific interactions between mesocarnivores at small scales, we expect that coyotes and bobcats act as potential intraguild predators and predict that gray fox and red fox occupancy will be negatively related to the occupancy of coyotes and bobcats. Additionally, we predicted that gray fox and red fox occupancy will be negatively related to increased coyote abundance. We predicted that raccoons will not be significantly impacted by interspecific interactions. Based on these expectations related to habitat and interspecific interactions, we predicted that red foxes would be most likely to occupy the same site as potential intraguild predators when urbanization is higher and that all species will be more likely to co-occur in areas higher habitat quality.

2.3 Methods

2.3.1 Study Area

The extent of our study area comprised most of the eastern U.S.A (Figure 2.5). All sites were located in the eastern temperate forest ecoregion (Omernik et al. 2017). This region can be divided into smaller ecoregions. To avoid confusion between these sub-regions and our total study area, when referring to the full extent of our study area, we will use the term eastern U.S.A. Despite the predominance of forest cover, land use in this portion of the eastern U.S.A. has changed dramatically in the preceding 50 years, with urban cover doubling and cropland declining between one fifth and one half (Brown et al. 2005).

2.3.2 Data Collection

We collected data on the presence and absence of coyotes, bobcats, gray foxes, red foxes, and raccoons at 170 sites across multiple landscapes in our study area (121 were sampled during 2012 and 49 were sampled during 2013. Data in this study came from The Appalachian Eagle project (http://www.appalachianeagles.org). This project's original goal was to use citizen science based camera trapping to photograph and determine the distribution of Golden Eagles throughout the eastern U.S.A. The project additionally collected data on many other species, including many mesocarnivores. The Appalachian Eagle project was designed to meet the challenges of large scale monitoring efforts (Lindenmayer and Likens 2010). The use of volunteer camera trappers allows researchers to remotely collect data in many landscapes across a large spatial extent (Silveira et al. 2003, Silvertown 2009). Data collected by remote camera trapping can be used to estimate both site occupancy and abundance (O'Connell et al. 2011).

Participants of the Appalachian Eagle project collected all photographic data used in this study. Volunteers placed cameras on a tree or post approximately 3' from the ground to view as much of the site as possible. Project leads asked volunteers to select sites that improved the chances of photographing Golden Eagles. Thus, they selected sites near wooded edges or in small clearings and generally at locally high elevations such as on top of a hill. Volunteers were instructed to bait sites with deer carcasses collected as roadkill. At least one carcass was placed at each site in the path of the camera. Volunteers were also instructed to operate sites for 2 to 4 weeks sometime between December 1st and April 15th. Volunteers sent images to the project lead where they were imported into a database and each image was labeled for the presence of coyotes, bobcats, gray foxes, red foxes, and raccoons. Additionally, we estimated the number of coyote visiting the site each day based on the maximum number of coyote seen in a single image during each day.

The sampling protocol presents several constraints that make the data from this study more appropriate for occupancy at this large scale than one based on local or microhabitat features. First, site selection cannot be considered random because the choice of site was meant to attract eagles. Second, site selection was shaped by the availability or discretion of each volunteer, so sites were often at property that could be easily accessed by the volunteer such as open fields or state land in the case of volunteers who worked for state wildlife agencies. Third, baiting the sites with a strong attractant enhances the detection power of cameras for species present near the site. Individuals visiting the site are likely to be photographed on the carcass and an attractant will draw in animals from a larger area around the site (Burton et al. 2015). These considerations bias each site toward conditions most suitable for detecting Golden Eagles. However, the survey protocol does not affect whether species are present within the landscape, so occupancy patterns within the eastern U.S.A should be unaffected.

2.3.3 Habitat Covariates

We began collecting habitat data by considering the scale at which to collect habitat covariates. The critical range at which landscape features will affect mesocarnivore occupancy was uncertain given that baiting may result in species being detected from far away and each species may have differing home ranges. We selected multiple scales as buffers around each site to collect habitat data based on the home range of each species. Buffers were based on the lowest, average, and highest reported home range for coyotes (Person and Hirth 1991, Bekoff 2003, Atwood 2004), gray foxes (Fritzell and Haroldson 1982, Harrison 1997), red foxes (Kurki et al. 1998, Walton et al. 2017), bobcats (Litvaitis et al. 1986, Reed et al. 2017), and raccoons (Gehrt and Fritzell 1997, Prange et al. 2003). Overlap in home range size resulted in seven scales, five of which were within the range of many species (25 km2, 10 km2, 5 km2, 2 km2, and 1 km2) and two representing larger potential bobcat home ranges (100 km2 and 200 km2). Ultimately, we estimated the scale at which each variable performed best in single species occupancy models for each species by testing each scale and selecting the scale that best fit the data based on Akaike information criterion (AIC) values (Slover and Katzner 2016).

We chose covariates characterizing the composition of land cover surrounding each site (Table 2.4). Habitat covariates had the most empirical support as factors impacting each species presence. We assessed the land cover at each site based on data from the national land cover database (NLCD 2011; Xian et al. 2011). We drew buffers around each site in the study using the buffer tool in ArcMap 10.2 (ESRI 2011). In each of these buffers, we estimated the percentage of each land cover type using tools in geospatial modeling environment (Beyer 2012). At each scale, we estimated the percentage of forest habitat as the proportion of deciduous, evergreen, mixed and total forest cover at each site (Kays et al. 2008, Temple et al. 2010). We also determined the proportion of urban cover (Lesmeister et al. 2016) and agricultural cover at each site (Gehring and Swihart 2003). Finally, we determined the proportion of edge habitat surrounding each site based on the percentage of forest habitat bordering agricultural and urban cover (Kurta 2004, Beasley et al. 2007).

We also collected covariates based on the distance from each camera site to the nearest urban area (Kowalski et al. 2015), road (Riley et al. 2006), and water source (Way et al. 2001). Predicting the impacts of urbanization is complicated by two factors: uncertainty in what components of urban landscapes species respond to and determining what level of human development constitutes, from a wildlife perspective, urbanization. To resolve this uncertainty, we used multiple covariates to classify distance to urbanization. We used map data for the landscape surrounding each site that incorporated urban boundaries defined by the U.S.A. census bureau (U.S. Census Bureau 2015), all urban cover (NLCD), and only high intensity urban cover (NLCD). The distance from each site to the nearest pixel of each urban classification was estimated as a separate covariate. Finally, we classified each site as greater than (1) or less than (0) potential threshold distances similar to what have been found for other landscape features (Radford and Bennet 2004). We also estimated the distance from each site to the nearest waterbody (Litvaitis and Shaw 1980, Harrison 1987, Way et al. 2001). Data for the distance to nearest waterbody came from the national hydrography dataset (USGS 2014). The distance from every site to the nearest of these features was obtained using the near tool in ArcMap 10.2. We tested for collinearity between all variables and did not include any two variables with a correlation above 0.7 in a single model (Dormann et al. 2013).

We conducted preliminary analysis of the data to test for spatial autocorrelation among sites. We used a partial mantel test to estimate the distance at which spatial autocorrelation might exist between habitat covariates among the 204 sites sampled during the 2012 and 2013 sampling year using the “ecodist” package in R (Goslee and Urban 2007). We tested all covariates and removed sites to avoid autocorrelation between any habitat characteristics. We found potential autocorrelation of covariates for sites closer than 5000 m. If two sites were closer than 5000 m then one site was selected randomly and removed. Therefore, we removed 34 sites, leaving 170 for analysis.

2.3.4 Coyote Abundance Index

We estimated the abundance of coyote at each site to further test the impacts of increased competition with coyote on the occupancy of other mesocarnivores. We used an n-mixture model (Royle and Nichols 2003) to estimate site level abundance based on the maximum number of coyote seen at each site during each sample day. The n-mixture model assumes that each site has a latent abundance that is estimated through repeated daily counts of the number of individuals observed at the site to estimate the detection rate at the site. Based on the record of abundances at each site and the estimated detection rate, our models generated an estimated abundance by assuming abundances were distributed according to a poisson distribution. N-mixture models have received criticism based on the accuracy of their abundance estimates (Barker et al. 2017). However, for the purposes of our models, even a relative measure of abundance provides inference about the effects of increased coyote abundance. All models for this analysis were run in the “unmarked” (Fiske and Chandler 2011) package in R 3.3.2 (R Core Team 2017).

2.3.5 Ecoregions

We classified each site based upon ecoregion to account for unexplained spatial effects that could be attributed to variation throughout our study area. The extent of our study area included areas in which habitat effects and interspecific interactions could potentially differ. This presents a problem because mesocarnivores may respond to these factors differently in different ecoregions. These differences can potentially mask the significance of a covariate or even change the direction of the effect. We collected ecoregion data to check the study sites for stationarity (Wagner and Fortin 2005). We assigned each site to a sub-region based on which level III ecoregion in which it was located (Omernik et al. 2017) We tested the performance of models based on subsets of the data included only the sites from each of these sub-regions.

2.3.6 Multispecies Models

We used multispecies occupancy models (Rota et al. 2015) to evaluate the effects of habitat and interspecific interactions on the mesocarnivore community. Multispecies models evaluate occupancy by generalizing Mackenzie et al.'s (2002) single-species model to two or more species. We assume the latent occupancy is a multivariate Bernoulli random variable and fit covariates with a multinomial logit link function. This model is parametrized to estimate the probability of occupancy for each species and the probability of co-occupancy of each species pair. We evaluate the importance of habitat for each species in these models by modelling the effect of habitat covariates on each species occupancy probability. We evaluate the importance of interactions between each species pair by comparing the performance of models with and without co-occupancy parameters. We evaluate the effect of habitat on interspecific interactions by modelling the effect of habitat covariates on each species co-occupancy.

2.3.7 Modelling Overview

We fit models with a multi-stage approach making use of single- and multi-species occupancy models. To understand the habitat associations of each species we tested the effect of habitat covariates on each species occupancy. To understand the effects interspecific interactions, we tested the significance of co-occupancy terms in multi-species models. We also tested the impact of increased coyote abundance on the occupancy of each species. To understand the effects of habitat on interspecific interactions, we tested the impacts of habitat covariates on species co-occupancy. We modeled the co-occupancy of each species pair as a function of urban features and preferred habitat. In every step, we assessed the performance of models with AIC.

2.3.8 Habitat Associations of Mesocarnivores

To understand the habitat associations of each species, we tested the effect of habitat covariates on the occupancy of each individual species. To estimate the best reduced habitat model, we used single-species models to compare the performance of models containing all potential covariates for each species. We selected the best performing model as the best reduced habitat model based upon AIC values. We ran single-species models in program PRESENCE 7.1 (Hines 2006). We tested the performance of each species-specific habitat model in multi-species models. Multi-species models contained parameters for the occupancy of each species and co-occupancy of each species pair. Multi-species habitat models were implemented by including species specific habitat covariates (habitat) or no habitat covariates (null) on each species occupancy. We ran multi-species models R (R Core Team 2017) with the package rSTAN (Carpenter et al. 2017).

2.3.9 Effects of Interspecific Interactions on Co-occupancy

To understand the nature of interspecific interactions, we tested the significance of interactions between the presence of species pairs. We compared the performance of models containing co-occupancy parameters for each species pair in rSTAN. The simplest models contained a co-occupancy parameter between two species (1 interaction parameter) and models with more species contained co-occupancy parameters for each species pair. We tested all combinations of pairwise interactions up to the full model with interactions between all species. We additionally tested the effect of increased coyote abundance on each species occupancy. We included coyote abundance index as a covariate of each species occupancy. We tested all combinations of species up to a model including coyote abundance index as predictor of each species occupancy.

2.3.10 Effect of Habitat on Interspecific Interactions

To understand how interspecific interactions changed as a function of habitat, we used multi-species models to test the impacts of habitat covariates each species pairs' co-occupancy. To test the effects of urbanization on interspecific interactions, we ran models containing proportion of urban cover and distance to urban as covariates of co-occupancy for each species pair. Each model only included urbanization covariates for at most one species pair. To test the impacts of suitable habitat on interspecific interactions, we ran models containing each species habitat associations as covariates of co-occupancy for each species pair. For each species pair, we ran a model containing covariates from the top habitat model for each species in the pair. We ran models for interactions between each species pair, but only included habitat for one species pair per model.

2.3.11 Validation

We validated models with data withheld from original modelling. We used 50 sites resampled during 2013 to validate models built with our original data. We generated predicted occupancy probability estimates based upon the covariate data collected at each additional site. We compared the predicted occupancy to the true occupancy, which was determined based on whether a species was detected at a site. We produced ROC curves using the R package “pROC” (Robin et al. 2011) and calculated AUC values determine the performance of each model.

2.4 Results

2.4.1 Habitat Associations

We found that habitat variability in the eastern U.S.A significantly impacted the occupancy of all mesocarnivore species. The top single-species model for each species contained between one and three covariates (Table 2.1). The top performing multi-species habitat model was the full model including habitat covariates of each species (Table 2.2). Some species habitat models represented a larger portion of model weight than others. Models that included habitat covariates for coyotes, bobcat, red foxes, or raccoon each had a combined model weight of at least 0.97. Models of gray fox habitat had a lower combined model weight of 0.77. For each model, most variables were significantly related to mesocarnivore occupancy (Figure 2.1). Only distance to water as a covariate on coyote occupancy and distance to road as a covariate on raccoon occupancy were non-significant. Coyote occupancy was directly related to the proportion of total forest cover ($\beta = 0.80$, SE = 0.28). Bobcat occupancy was inversely related to the proportion of agricultural cover ($\beta = -0.61$, SE = 0.22). Gray fox occupancy was directly related to the proportion of forest cover ($\beta =-0.61$, SE = 0.26) and inversely related to distance to water ($\beta = -0.85$, SE = 0.28). Red foxes were less likely to occupy sites with greater forest cover ($\beta = -0.47$, SE = 0.18) or further from urban cover ($\beta = -0.44$, SE = 0.17). Raccoons occupancy was positively related to agricultural edge (0.83, SE = 0.19) and the proportion of urban cover ($\beta = 0.50$, SE = 0.25). Relationships between habitat covariates and coyote occupancy did not differ significantly between sub-regions (Table 2.6)

2.4.2 Interactions

We found evidence of interactions between species presence for few species pairs. The top interaction model included the co-occupancy parameter between coyotes, bobcats, red foxes, and raccoons. This single model had a model weight of 0.95. Only red foxes avoided the presence of potential intraguild predators. Bobcat and red fox occupancies were negatively related (β = -

1.12, SE = 0.41). Also, bobcats (β = 1.92, SE = 0.40), gray foxes (β = 0.77, SE = 0.38), and red foxes (β = 1.34, SE = 0.42) were all more likely to occupy sites in the presence of raccoons. However, models including gray fox and raccoon co-occupancy did not have a large combined model weight (0.039). No species had a significant interaction effect with coyote presence alone, however gray foxes and red foxes avoided increased coyote abundance. The top model including coyote abundance index as a covariate of species occupancy included the effects of coyote abundance index on bobcat, gray fox, and red fox occupancy, but not raccoon occupancy.

2.4.3 Effect of Habitat on Interactions

Urbanization and habitat suitability impacted interactions between many mesocarnivore pairs. Interactions with coyotes were only impacted by urbanization for red foxes. Coyote and red fox co-occupancy was positively related to the proportion of urban cover (β = 0.017, SE = 0.0087) and negatively related to the distance to urbanization (β = -0.30, SE = 0.13). At low levels of urban cover, red foxes avoided coyote presence however high urban cover the occupancy probability of red foxes was higher in the presence of coyote (Figure 2.2). Interactions between bobcats and some smaller species were impacted by the amount of urban cover. Bobcat and red fox co-occupancy (β = 0.016, SE = 0.0082) as well as bobcat and raccoon co-occupancy (β = 0.019, SE = 0.0082) were positively related to the proportion of urban cover. Red foxes avoided bobcats at low urban cover, but urbanization facilitated coexistence with bobcats, similar to the pattern observed with coyote (Figure 2.2). Gray fox and red fox co-occupancy was negatively related to the distance to urban features (β = -0.51, SE = 0.26). Red fox occupancy was lower in the presence of gray foxes, however as the distance to urban decreased then the strength of competition decreased and the likelihood of these species co-occurring increased. Red fox and raccoon co-occupancy was positively related to the proportion of urban cover (β = 0.017, SE = 0.0092).

Non-urban habitat preferences also impacted the co-occupancy of many mesocarnivores. Coyote and bobcat co-occupancy was positively related to total forest cover (β = 0.53, SE = 0.18) and distance to water (-0.64, SE = 0.25). Total forest cover was also directly related to coyote and raccoon co-occupancy (β = 0.46, SE = 0.21). Bobcat and raccoon co-occupancy was inversely related to the proportion of agricultural cover (β = -0.52, SE = 0.30). Suitable gray fox habitat decreased the strength of competition between gray foxes and higher trophic level species. Gray fox and coyote co-occupancy was positively related to forest cover (0.55, SE = 0.22) and negatively related to distance to water (β = -0.85, SE = 0.28). Gray fox and bobcat co-occupancy was negatively related to distance to water (-0.95, SE = 0.36). Total forest cover also positively impacted the co-occupancy of gray foxes and raccoons (β = 1.15, SE = 0.37). No habitat characteristics significantly impacted the co-occupancy of red foxes and other species other than urbanization measures. Raccoons coexisted with other mesocarnivores more often when habitat was more suitable. Agricultural edge habitat was positively related to the co-occupancy of raccoons and coyotes (β = 0.67, SE = 0.19), raccoons and gray foxes (β = 0.67, SE = 0.23), and raccoons and red foxes (β = 0.82, SE = 0.21).

2.4.4 Validation

We found that models performed well for predicting mesocarnivore occupancy for validation sites. Model validation performed best for red foxes and worst for raccoons. Area under the curve (AUC) scores for each species were: 0.7942 for coyotes, 0.8033 for bobcats, 0.6881 for gray foxes, 0.8697 for red foxes, and 0.6711 for raccoons.

2.5 Discussion

We found support for our hypotheses that of mesocarnivore select habitat that reduced the strength of competition. Increased habitat quality was positively associated with co-occupancy of all species pairs in this study, suggesting that competition may decrease in better quality habitat (Swanson et al. 2016). Despite this common effect of increased habitat quality on species interactions, mesocarnivores varied in their specific habitat associations and relative trophic level (Newsome and Ripple 2015). For example, we found no negative interactions between coyotes and bobcats or between gray foxes and red foxes but we found strong negative interactions between bobcats and red foxes and that increased coyote abundance had a negative impact on both gray fox and red fox occupancy (Fedriani et al. 2000). Based on these results we concluded that larger species were likely impacting smaller species through top down predation pressure (Arim and Marquet 2004) and, consequently, increased urbanization was only likely to reduce the strength of these predator prey interactions (Janssen et al. 2007). Interactions also differed depending upon the reaction of the potential prey to the potential predator (Jones et al. 2016).

Specifically, habitat resulted in more changes to interspecific interactions between red foxes and potential intraguild predators than gray foxes and potential intraguild predators.

Neither habitat nor interspecific interactions alone could explain differences among members of the mesocarnivore community. For example, gray foxes and red foxes differ in their success in this region and in human modified areas generally (Alessi et al. 2012, Willingham 2008, Bateman and Fleming 2012). Gray foxes preferred forested habitats but responded neither positively or negatively to urban cover. Red foxes responded negatively to forest cover and instead selected for areas closer to urban features. Based on habitat alone, given the predominance of forest cover in this region, one may naively expect gray foxes to occupy a greater portion of the eastern U.S.A. Additionally, it is unclear why red foxes would not only tolerate but select for urban areas given the risks posed by urbanization (Snow et al. 2012). Gray foxes and red foxes also differ in terms of interactions with other species. Red fox occupancy was negatively related to the presence of predators including both bobcat and coyote. While coyotes were too widespread to completely avoid, red foxes generally did not occupy areas where coyote were most abundant. Gray foxes also responded negatively to increased coyote abundance but not to coyote or bobcat presence. The explanation for these trends can be reconciled by considering both habitat and interactions simultaneously (Rota et al. 2016). Gray fox selected for the same habitat types as coyote and were likely to occupy sites with coyote present particularly when forest cover was high. However, we did not find gray foxes in landscapes where competition with coyote was intense. Presumably, gray foxes were unable to use alternative habitat to avoid coyote and these results are consistent with this explanation for gray fox declines. In contrast, competition and predation drove red foxes’ association with urban areas despite the potential risks presented by urbanization. In urban areas, competition with coyotes and bobcats was reduced, therefore red foxes could use these areas as refuges in a way that gray foxes could not (Ordenna 2011).

Species differed in the habitat types they selected as well as their propensity to use urban habitats. Coyotes and gray foxes selected for the most similar habitat between any species pair we studied. In the eastern U.S.A., coyotes and gray foxes represent the greatest amount of niche overlap among these species. The lack of niche partitioning between these species contributes to the high intensity of competition and intraguild killing of gray foxes by coyotes (Fedriani et al. 2000, Schuette et al. 2013). We did not find evidence of urban avoidance across the eastern U.S.A. At smaller scales, some mesocarnivores are known to respond to urbanization (Ordenna et al.

2010), however at this scale no species avoided urban cover or urban features and only bobcats avoided human modified agricultural landscapes. This trend could be the result of the limited range of urbanization tested in our sample, however within this range we did detect positive responses to urban cover and impacts of urban cover on interactions. The positive association of some mesocarnivores with urban areas may be related to decreased intraguild predation and competition urban areas. Red foxes relied most heavily on these urban refuges, but raccoons also used urban landscapes as well as edge habitat near agricultural cover. Despite potential direct risks (Kamler and Gipson 2004, Snow et al. 2012), these areas may act as refuges for many reasons. Urban and agricultural areas may have food resources that can be consumed by generalist species (Reshamwala et al. 2018), allowing them to avoid competing for other resources. Many species have smaller home ranges in urban areas, resulting in less home range overlap and decreased competition (Mueller et al. 2018). While other species, like gray foxes, did not avoid urban areas explicitly, relative inability to make use of urban habitat may limit their ability to avoid predators.

We did not find differences in the effect of covariates between the sub-regions in our study area. Given the extent of our study area, we considered that there may be variability in our data related to spatial effects not explored in our occupancy analysis (Wagner and Fortin 2005). The species in this study have geographic ranges greater than the extent of the eastern U.S.A. Mesocarnivores may differ between the eastern and western U.S.A. in many ways (Way 2007). While our study area comprised only the eastern U.S.A., habitat potentially may have impacted mesocarnivores and interactions differently depending upon which sub-region within the eastern U.S.A that the site was situated. However, we found that the relationship between habitat covariates and each species occupancy probability did not differ between these sub-regions. Non-stationarity has been shown to impact model performance for other species or in other systems (Gering et al. 2003, Osborne et al. 2007). In contrast to these studies, our results support the idea that, in the eastern U.S.A, and at the scale of our study, mesocarnivores responded to habitat consistently.

Interspecific interactions in our study were consistent with the expectations of mesopredator release. We only found significant negative interactions between potential intraguild predators and their potential prey. Competition likely exists between all species within the mesocarnivore community (Caro and Stoner 2003), however mesocarnivores only responded with spatial avoidance when there was potential for intraguild predation (Ripple and Beschta 2004). Our results support the idea that coyotes may fill the role of a top predator of smaller mesocarnivores (Gompper 2002) Bobcats were less prevalent and therefore more easily avoided by other mesocarnivores (Clare et al. 2015). Despite evidence in other studies that bobcats may also be killed by coyotes, our results indicate bobcats occupy a similar role as an intraguild predator (Wilson et al. 2010, Witczuk et al. 2015). In the absence of top predators, these species have likely increased in distribution and abundance so that they provide strong top down effects. As a result, gray foxes and red foxes respond to coyotes and bobcats with spatial avoidance or altered habitat selection. Raccoons may avoid competition because of generalist feeding behavior or compensate for predation because of their life history (Prange et al. 2003). Raccoon distributions may be related to high abundance, however raccoons were not present at all sites, and their habitat associations may imply raccoons selected for other factors common among mesocarnivore but not examined in this study.

Ultimately, our results indicate that both increased urbanization and the loss of top predators shape the distributions of extant mesocarnivores across the eastern U.S.A. Contrary to findings at other scales, neither factor alone structured this community more strongly (Gompper et al 2016, Rich et al. 2017). Rather, to understand the structure of the mesocarnivore community we needed to understand how these factors worked in concert. We found evidence that the mesocarnivore guild was structured by top down effects. Mesocarnivores in our study were either potential intraguild predators (coyote, bobcat) or intraguild prey (gray fox, red fox). Other studies have proposed that the loss of top predators in this system has resulted in new top predators and cascading effects across trophic levels (Newsome and Ripple 2014). Top down effects were important both directly in terms of predator avoidance and indirectly through behavioral changes that drive habitat selection. Mesocarnivores have been recognized as the beneficiaries of urbanized landscapes relative to other species, however our findings suggest that in the eastern U.S.A., the impacts of urbanization depend on how urbanization affects the interactions between members of the mesocarnivore community.

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Table 5 Top performing habitat models for each species from single-species models.

Species	**Model**
Coyote	Total Forest Cover; Distance to Water
Bobcat	Agricultural Cover
Gray Fox	Total Forest Cover; Distance to Water
Red Fox	Total Forest Cover; Distance to Urban
Raccoon	Agricultural Edge; Urban Cover; Distance to Road

Table 6 Top performing models for each step of analysis. A) Comparison of the top models including habitat covariates for each species. These models tested the relationship between each species occupancy and habitat covariates. The model name indicates the species for which habitat covariates were included. B) Comparison of the top models of species interactions. Interactions were tested by comparing the performance of models including the co-occupancy of each species pair. The model name indicates species for which co-occupancy parameters were included. C) Comparison of the top models of the impact of coyote abundance index on species occupancy. The effect increased coyote abundance was tested by including the coyote abundance index as a covariate on each species occupancy. The model name indicates species for which coyote abundance index was included as a covariate. Comparison of the top presence only interaction models. Models included make up 0.95 model weight.

Model Name	**-2 Log Likelihood**	**ΔAIC**	**Weight**
A)			
Coyote, Bobcat, Gray Fox, Red Fox, Raccoon	20566.55	0	0.74
Coyote, Bobcat, Red Fox, Raccoon	20584.74	2.33	0.23
B)			
Coyote, Bobcat, Red Fox, Raccoon	20584.14	0	0.95
Coyote, Bobcat, Gray Fox, Red Fox, Raccoon	20566.55	7.33	0.024
C)			
Bobcat, Gray Fox, Red Fox	20560.47	0	0.89
Bobcat, Gray Fox, Red Fox, Raccoon	20552.88	5.66	0.052
Gray Fox	20567.07	7.85	0.018

Table 7 Top performing models comparing the impacts of habitat on species interactions A) Top performing models testing the impacts of urban cover on species interactions. Model names indicate which species co-occupancy included the covariate urban cover. B) Top performing models testing the impacts distance to urban on species interactions. Model names indicate which species co-occupancy included the covariate distance to urban. C) Top performing models testing the impacts of non-urban habitat on species interactions. Model names indicate which species co-occupancy included habitat covariates. Models included make up 0.95 model weight.

Model Name	**-2 Log Likelihood**	**ΔAIC**	**Weight**
A)			
Bobcat-Gray Fox	20661.38	0	0.87
Coyote-Red Fox	20650.18	4.94	0.073
Red Fox-Raccoon	20647.49	7.91	0.017
B)			
Gray Fox-Red Fox	20655.14	0	0.66
Bobcat-Red Fox	20659.22	2.91	0.15
Bobcat-Raccoon	20658.01	5.17	0.050
Coyote-Gray Fox	20659.7	5.49	0.042
Red Fox-Raccoon	20654.79	6.02	0.033
Coyote-Bobcat	20655.75	7.2	0.018
C)			
Coyote-Raccoon	20632.15	0	0.80
Red Fox-Raccoon	20625.99	2.83	0.19

Table 8 Covariates of the occupancy and detection of coyote and gray fox in the Eastern United States. Habitat covariates include measures of the proportion of the landscape surrounding each site belonging to a particular cover type and the distance from each site to the nearest habitat feature. Proportion landscape variables were all assessed at five scales measuring $1km^2$, $2km^2$, $5km^2$, $10km^2$, and $25km^2$, but are reported for the largest range. Distances are in meters

Covariate	**Mean**	**Standard Deviation**	**Maximum**	**Minimum**	**Source**
Proportion Total Forest Cover	0.751	0.263	0.996	0.00552	Kays et al. 2008 Temple et al. 2010
Proportion Deciduous Forest Cover	0.657	0.259	0.983	0	Kays et al. 2008 Temple et al. 2010
Proportion Evergreen Forest Cover	0.0467	0.067	0.400	0	Kays et al. 2008 Temple et al. 2010
Proportion Mixed Forest Cover	0.0468	0.0718	0.508	0	Kays et al. 2008 Temple et al. 2010
Proportion Agriculture Cover	0.121	0.171	0.851	0	Gehring and Swihart 2003
Proportion Urban Cover	0.0472	0.0475	0.351	0.000658	Cove et al. 2012, Lesmeister et al. 2016
Distance to nearest water source	1,328	1108	4,628	27	Litvaitis and Shaw 1980, Harrison 1987
Distance to nearest urban boundary	14,037	10,694	46,239	460	Kowalski et al. 2015
Distance to nearest high intensity urban cover	2,447	1,908	11,136	147	Kowalski et al. 2015, Ordenna et al. 2010, Gompper et al. 2016
Distance to nearest of any urban cover	1,176	913	3,994	56	Kowalski et al. 2015, Ordenna et al. 2010, Gompper et al. 2016
Distance to nearest road	3,317	2,483	12,578	56	Riley et al. 2006
Coyote Abundance Index	3.22	2.39	12.80	0.00014	Lesmeister et al. 2016

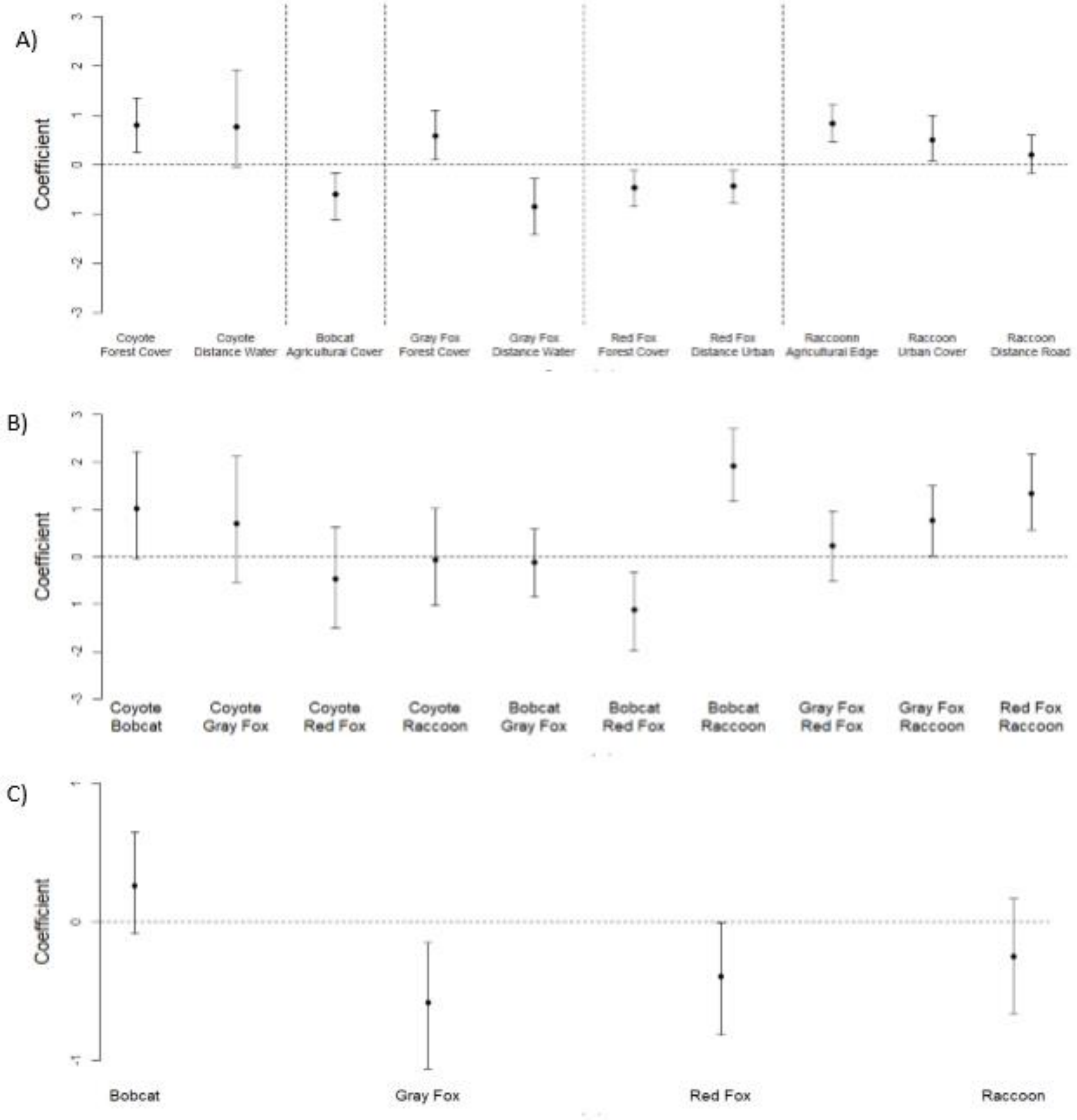

Figure 7 Beta coefficients for each habitat covariate on occupancy (A), species co-occupancy (B), the effect of urban cover on co-occupancy (C), and the effect of distance to urban on co-occupancy (D). Estimates are model averaged from all models containing that covariate. Bars represent 95% credible intervals around the estimate. Coefficients that are above and do not overlap 0 had a significant positive impact on occupancy. Coefficients that are below and do not overlap 0 had a significant negative impact on occupancy.

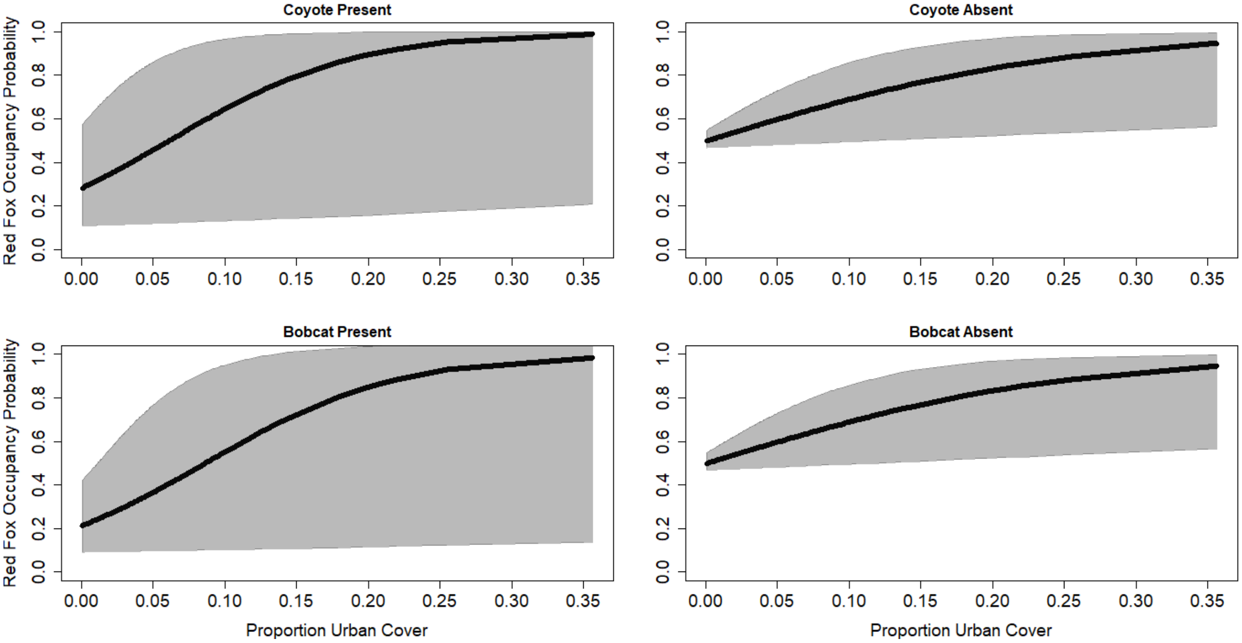

Figure 8 Red fox occupancy related to the proportion of urban cover conditional on the presence (right) or absence (left) of coyote (top) and bobcat (bottom). Shaded areas represent the 95% credible interval surrounding occupancy estimates. Avoidance by red foxes in the presence of predators is stronger in areas with low urban cover.

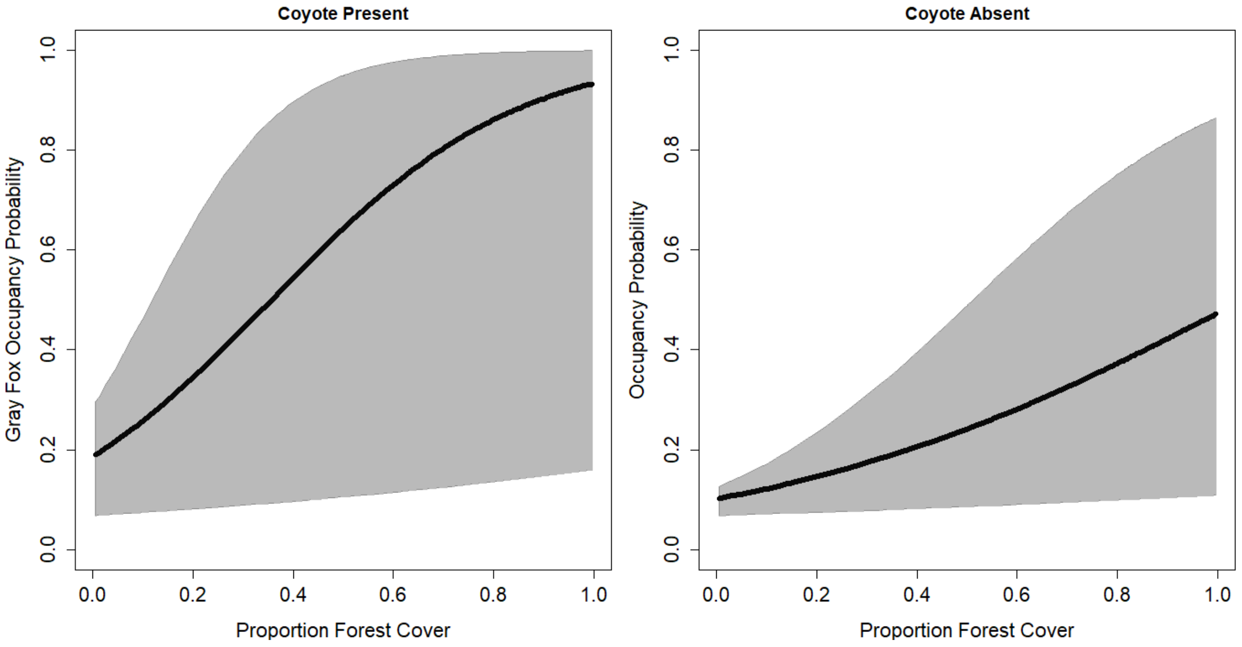

Figure 9 Gray fox occupancy related to forest cover conditional on the presence (right) or absence (left) of coyote. Shaded areas represent the 95% credible interval surrounding occupancy estimates. Gray foxes occupied sites with coyote in more forested areas.

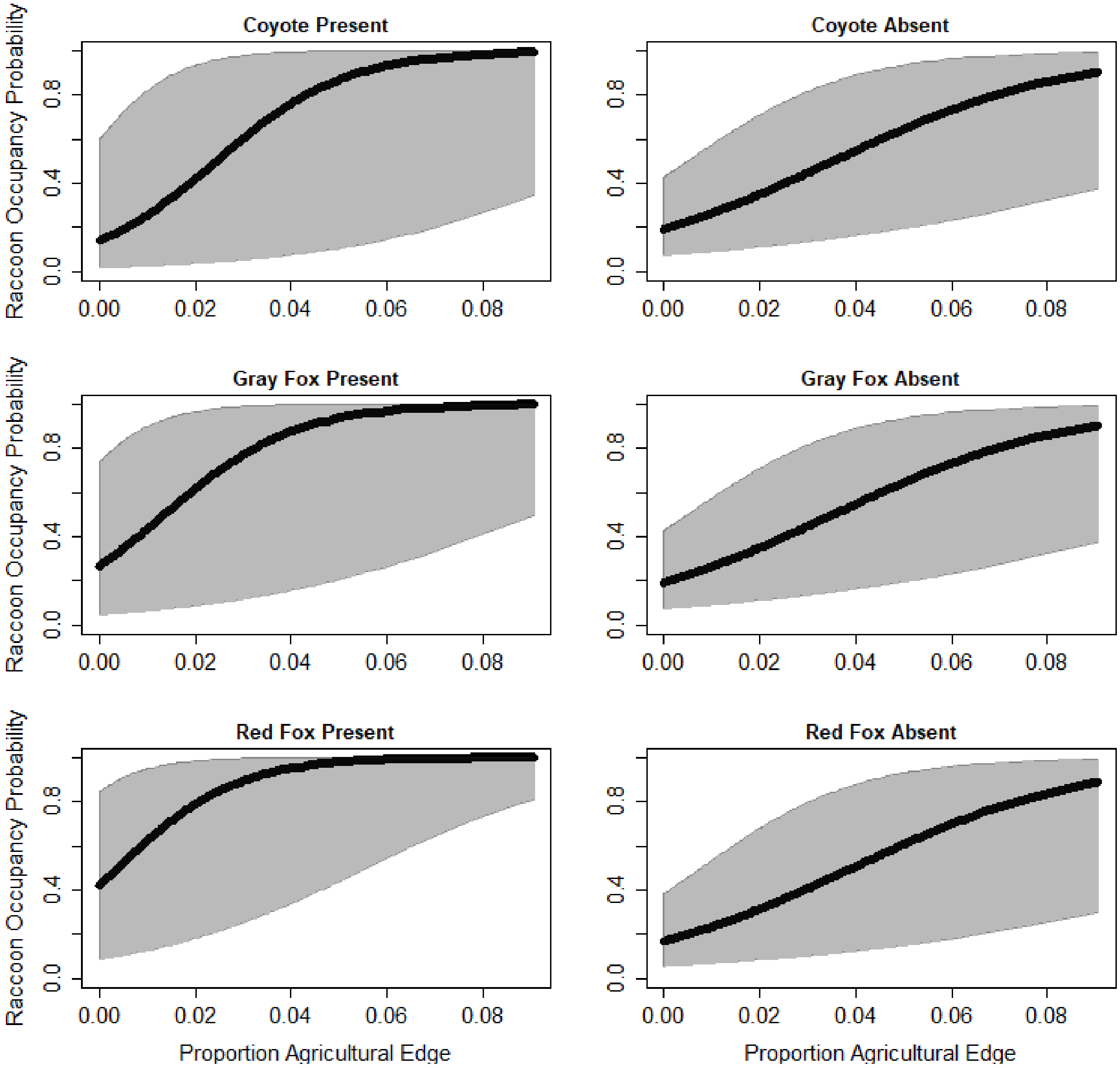

Figure 10 Raccoon occupancy related to agricultural edge conditional on the presence (right) or absence (left) of coyote (top), gray fox (middle), and red fox (bottom). The shaded areas represent the 95% credible interval surrounding occupancy estimates. Raccoons were positively related to agricultural edge habitat and the presence of other mesocarnivores.

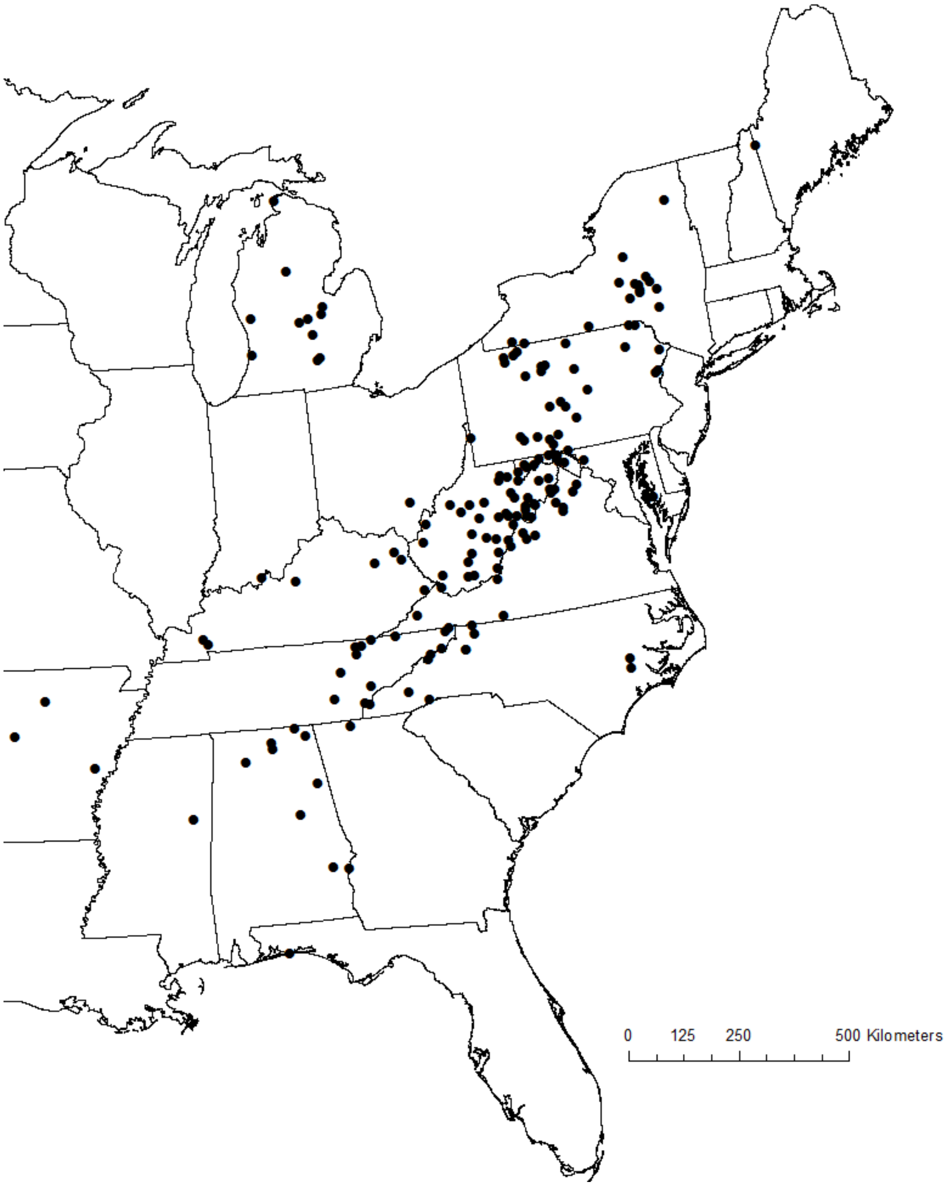

Figure 11 Distribution of sites throughout the study area in the eastern U.S.A.

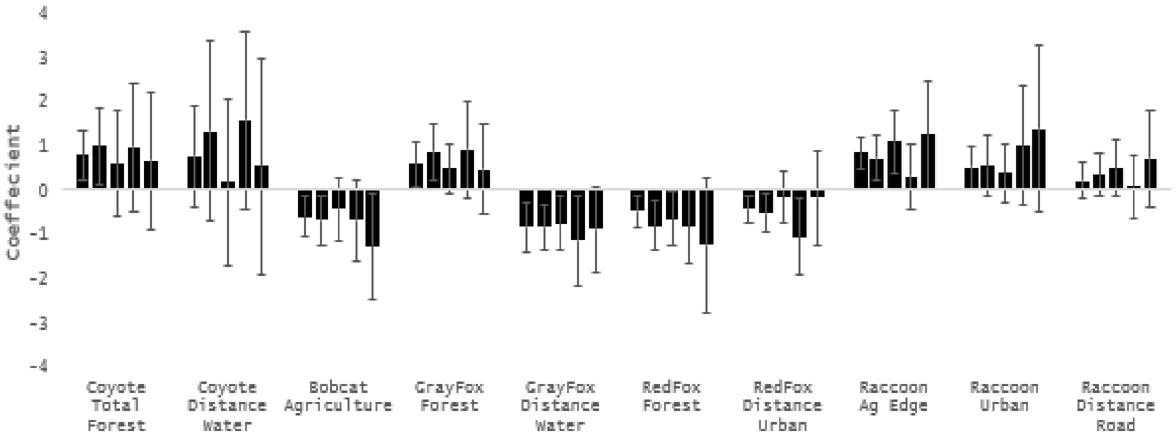

Figure 12 Performance of habitat covariates in across sub-regions (Omernik et al. 2017). The study area was divided into sub-regions and the performance of models was tested on the subset of sites contained within this sub-region. Coefficients are included for the entire study area and for each sub-region. Models and covariates did not perform significantly different in differing sub-regions implying there was not unaccounted for spatial heterogeneity.